





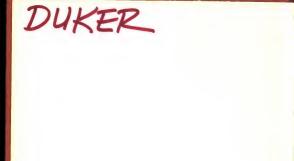
THE VERTEBRATE BODY





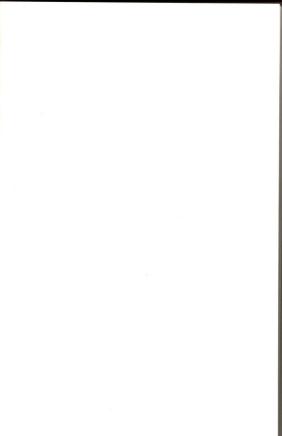
**Shorter Version** 

ROMER



















## THE VERTEBRATE BODY





THIRD EDITION

ILLUSTRATED

**Shorter Version** 

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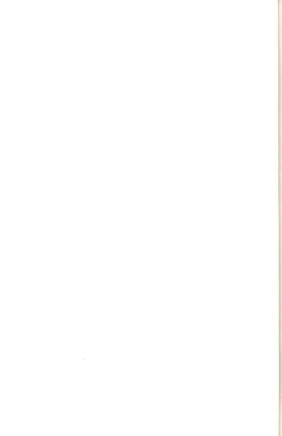
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### **PREFACE**

The publication of a shorter version of The Vertebrate Body some years ago, based on the second edition of that book, was due to the expressed desire for a text useful in courses with limited available time. The present revision, based on the third edition of the longer work, follows the patern of its predecessor. The first three chapters, including introductory and "natural history" topics, and the appendices, are reproduced here without change from the new third edition of the larger book. In the main body of the work, the full series of illustrations has been repeated, but the text has been cut oapproximately half length by the omission of details and matters of lesser interest. Much of the text is comparable to that of the previous edition, but numerous minor changes have been made throughout, parts of several chapters have been rewritten, and discussion of endocrine structures has been collected into a concluding chapter. A number of fillustrations have been modified and replaced, about a score of new figures added, and addition of color in several areas has, I hope, made for greater clarity.

My major debts to friends and associates for aid are expressed in the preface to the longer work.

ALFRED SHERWOOD ROMER



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## INTRODUCTION

This work is designed to give, in brief form, a history of the vertebrate body. Basic will be a comparative study of vertebrate structures: the domain of comparative anatomy. This is in itself an interesting and not unprofitable discipline. Of broader import, however, is the fact that the structural modifications witnessed are concerned with functional changes undergone by the vertebrates—changes correlated with the varied environments and modes of life found in the course of their long and eventful history. The evolutionary story of the vertebrates is better known than that of any other animal group, and vertebrate history affords excellent illustrations of many general biologic principles. Knowledge of vertebrate structure is of practical value to workers in many fields of animal biology. To the future medical student such a study gives a broader understanding of the nature of the one specific animal type on which his later studies will be concentrated.

For the most part (Chap. 6-17) the present volume is devoted to a consideration. seriatin, of the various organs and organ systems. In the present chapter is given a "bird's eye" view of vertebrate structure, together with certain introductory matters. Other early chapters discuss general or preliminary topics, including the evolutionary history of the vertebrates and their kin (Chap. 2 and 3); cells and tissues as the basic structural elements (Chap. 4); and embryonic development (Chap. 5).

#### THE VERTEBRATE BODY PLAN

Bilateral Symmetry. A primary feature of the vertebrate structural patters in the fact that members of this group are bilaterally symmetric, with one side of the body essentially a mirror image of the other. Vertebrates share this type of organization with a number of invertebrate groups, notably the annelid worms and the great arthropod phylum, which includes crustaceans, arachinds, inscets, and so forth. In strong contrast is the radial symmetry of coelenterates and echinoderms, in which the body parts radiate out from a central axis like the spokes of a wheel. The degree of activity of animals appears to be correlated with the type of symmetry which is present. The radiate echinoderms and coelenterates are in general stuggish types, slow-moving or fixed to the bottom or, if free-floating, mainly drifters with the current rather than active swimmers. Vertebrates, arthropods, and marine annelids are, on the other hand, generally active animals. Activity would seem to have been one of the keys to the success of the vertebrates and is in a sense as diaenostic as any anatomic feature.

Regional Differentiation. In any bilaterally symmetric animal we find some type of longitudinal division into successive body regions—in the annelid worms, for example, a rather monotonous repetition of essentially similar segments, or in insects a pattern in which such segments are consolidated into head, thorax, and abdomen. Vertebrates, too, have well-defined body regions, although these regions are not directly comparable to those of invertebrate groups.

There is in vertebrates a highly specialized head, or cephalic region; in this region are assembled the principal sense organs, the major nerve centers which form the brain, and the mouth and associated structures. Here, as in all bilaterially symmetric animals (even a worm), there is a strong tendency toward cephalization—a concentration of structures and functions at the anterior end of the body.

In all higher, land-dwelling vertebrate groups a neck is present behind the head; this is little more than a connecting piece, allowing movement of the head on the trunk. The presence of a neck region is not, however, a primitive vertebrate feature. In lower, water-breathing vertebrates this section of the body is the stout gill region, containing the breathing apparatus. The appearance of a distinct neck occurs only with the shift to lung breathing and the reduction of the gills.

The main body of the animal, the trunk, is the next following region; this terminates in the neighborhood of the anus or close. Within the sout trunk are the body cavities containing major body organs, the viscera. In mammals the trunk is divisible into thorax and abdomen, the former containing the heart and lungs within a rib basket, the latter enclosing most of the digestive tract; there is, however, no clear subdivision here in lower vertebrates.

In most bilateral invertebrates the digestive tube continues almost the entire length of the body. Among the vertebrates, however, we find, in contrast, that the digestive tract and other viscera stop well short of the end of the body; beyond the trunk there typically extends a well-developed and or caudal region, with flesh and skeleton, but without viscera. The tail is, of course, the main propulsive organ in primitive water-dwelling vertebrates. In land animals it tends to diminish in importance, but is often long and stout at the base and well developed in many amphibians and reptiles. In mammals it is generally persistent, but is merely a slender appendage. In birds it is shortened and functionally replaced by the tail feathers, arising from its stump; in some forms—frogs, apes, and man—it is, excertionally, lost completely as an external structure.

Gills. The presence, in embryo if not in adult, of internal gills developed in a paired series of clefts or pouches leading outward from an anterior part of the gut—the pharynx—is one of the most distinctive features (perhaps the most distinctive feature) of the vertebrates and their close kin. In higher vertebrates the gills are functionally replaced by lungs, but gill pouches are nevertheless prominent in the embryo. In lower water-dwelling vertebrates gills are the primary breathing organs. Among small invertebrates, many with soft membranous surfaces can get enough oxygen through such membranes to supply their wants. But in forms with a hard or shell; surface, and especially in large forms, where the surface area is of course small compared with the bulk of the body, gill structures of some sort are a necessity. Typical invertebrate gills, as seen in crusta-

ceans or molluses, are feathery projections from the body surface. The vertebrate gill, however, is an internal development, connected with the digestive tube. Water enters the "throat," or pharynx (usually through the mouth), and passes outward through slits or pouches; on the surface of these passages are gill membranes, at which an exchange of oxygen from the water for carbon dioxide in the blood takes place. Quite in contrast is the gill function in certain lowly relatives of the vertebrates. There, as we shall see, the gills and gill slits are of primary importance in food collection—a fact tending to explain the unusual vertebrate condition of an association of the breathing organs with the digestive tube.

Notechord. In the embryo of every vertebrate there is found, extending from head to tail the length of the back, a long, flexible, rodilike structure—the notochord. In most vertebrates the notochord is much reduced or absent in the adult, where it is replaced by the vertebral column, or backbone. But it is still prominent in some of the lower vertebrates, and is the main support of the trunk in certain simply-built vertebrate relatives (such as Amphioxus) in which no vertebral column ever forms. So significant is this primitive supporting structure that the vertebrates and their kin are termed the phylum Chordata, a name referring to the presence of a notochord.

Nerrous System. Longitudinal nerve cords are developed in various bilaterally symmetric invertebrate groups. These, however, are frequently paired and may be lateral or ventral in position. Only in the chordates do we find developed a single cord, dorsally situated and running along the back above the notochord or the vertebrae. Invertebrate nerve cords are solid masses of nerve fisc, and supporting cells) running between equally solid clusters of nerve clist, termed ganglia. The chordate nerve cord is, in contrast, a hollow, nonganglionated structure, with a central, fluid-filled cavity. In various invertebrates the process of cephalization has tended to a concentration of nerve centers in a brainfile structure. Independently, we believe, the vertebrates have evolved a hollow brain, with characteristic subdivisions, at the anterior end of the hollow nerve cord—the spinal cord. Not exactly matched in any invertebrate group is a series of characteristic sense organs developed in the head region of vertebrates—paired eye and, primitively, a third, median eye, nasal structures, usually paired; paired ears with equilibirum as their primary function.

Digestive System. All metazoans (with degenerate exceptions) have some sort of digestive cavity with a means of entrance to and exit from it. In many of the more primitive metazoans there is but a single opening, serving as both mouth and anus. In vertebrates, as in other more progressive metazoans, there are separate

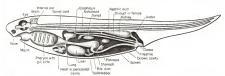


Fig. 1. Diagrammatic longitudinal section through an "idealized" vertebrate, to show the relative position of the major organs.

anterior and posterior openings. The mouth is situated near the front end of the body, typically somewhat to the underside. In arthropods and annelids the digestive tube reaches to the posterior end of the body. In vertebrates, however, this is not the case; the anus is situated at the end of the trunk, leaving, as we have seen, a caudal region in which the digestive tube is absent.

In most vertebrates the digestive tube is divided into a series of characteristic regions serving varied functions—mouth, pharyax, esophagus, stomach, and intestine (the last variously subdivided). In lower vertebrates the esophagus may be almost nonexistent, and in some groups the stomach even may be absent. In mammals and certain other vertebrates the digestive tract terminates externally at the anas. In most groups, however, there is a terminal gut segment, the cloaca, into which urinary and genital ducts also lead.

A liver which performs to some extent a secretory function, but is in the main a seat of food storage and conversion, is present in vertebrates as a large, single ventral outgrowth of the digestive tube. Somewhat similar but variable structures are present in many invertebrates.

Kidneys. Among invertebrates some type of kidney-like organs for the disposal of nitrogenous waste and the maintenance of a proper composition of the internal fluids of the body are often present, typically as rows of small tubular structures termed nephridia. Of chordates below the vertebrate level, Amphioxus has nephridia of a special type. In true vertebrates however, the kidney ubulas serving such a function are of a markedly different type and are characteristically gathered into compact paired kidneys, dorsal in position. Kidney ducts, of variable nature, lead to the cloacal region or to the exterior, and a urinary bladder may develop along their course.

Reproductive Organs. Male and female sexes are almost invariably distinct in the vertebrates, as they are in many invertebrate groups. The lissues containing the germ cells—the gonads—develop into either testis or orary. In all except the lowest vertebrates a duct system leads the eggs or sperm to or toward the surface (frequently by way of the cloaca); and in the female, special duct regions may be present for shell deposition or for development of the young.

Circulatory System. In vertebrates, as in many invertebrates, there is a well developed organ system containing a body fluid, the blood, with tubular vessels and a pump, the heart, to bring about its circulation. The heart in vertebrates is a unit structure, ventrally and rather anteriorly situated. In certain invertebrates the circulation is of an "open" type: the blood is pumped from the heart to the tissues in closed vessels, but is then released and makes its return to the heart by oozing through the tissues without being enclosed in vessels. In the vertebrates, as in some of the more highly organized invertebrates, the system is closed; not only is the blood carried by the arteries to the various organs, but the return to the heart, after passing through the tissues in small tubes, the capillaries, is also made in closed vessels, the veins. In most vertebrates lymph vessels are present as an additional means of returning fluid from the cells to the heart. Many invertebrates contain in their blood streams pigmented metallic compounds in solution which aid in the transportation of oxygen. Among vertebrates, almost exclusively, the iron compound hemoglobin is the oxygen carrier; and, further, this chemical is not free in the blood, but is contained in blood cells.

In annelids the circulation of the blood is in general forward along the dorsal side of the body, backward ventrally in its return to the tissues. The reverse is true of the vertebrates. The blood from the heart passes forward and upward

(primitively via the gills) and back dorsally to reach the organs of trunk and tail, and a major return forward—from the digestive tract—is ventral to the gut (although dorsal veins are important).

Celom. In certain invertebrates the internal organs are embedded in the body tissues. In others, however, there develop body cavities—colomic cavities—filled with a watery fluid, in which most of the major organs are found. This latter condition is present among vertebrates. A major body cavity—the abdominal cavity—occupies much of the trunk and contains most of the digestive tract; various other organs (reproductive, urinary) project into it. Anteriorly there is a discrete pericardial cavity enclosing the heart, and in mammals the lungs are contained in separate pleural cavities.

Muscles. Musculature in the vertebrates is of two types, striated and smooth (or nonstriated), the two differing sharply in minute structure and indistribution in the body. The former, roughly, includes all the voluntary musculature of the head, trunk, limbs, and tail, and the muscles of the gill region; the smooth musculature, more diffuse, is mainly found in the lining of the digestive tract. The musculature of the heart is in various respects intermediate in microscopic structure. The striated musculature of the trunk develops, unlike most other organ systems, as a series of segmental units.

Skeleton. Hard skeletal materials are present in all vertebrates, and in all except certain degenerate or (doubtfully) primitive groups consist in part, at least, of bone. Superficial skeletal parts, the deemal skeleton, correspond functionally to the "armor" of certain invertebrates, and are typically bony; internal skeletal structures, the endoskeleton, are formed as cartilage in the embryo, but are frequently replaced by bone in the adult. Cartilage-like materials are found in invertebrates. Bone, however, is a unique vertebrate tissue. It differs in texture and minute structure from the typical chitinous or calcareous skeletal materials of invertebrates, and, in the fact that the salts deposited in this tissue are mainly calcium phosphate, it differs from most (but not all) invertebrate skeletal structures—in which carbonate is the common calcium comoound.

Appendages. Two pairs of limbs, pectoral and pelvic, are found in most vertebrates in the form of fins or legs and become increasingly prominent in higher members of the group. They are, however, little developed or are absent in the lowest of vertebrates, living and extinct, and hence are not absolutely characteristic. Their structure (in contrast to arthropod limbs) includes internal skeletal elements, with muscles for their movement arrayed above and below.

Segmentation. The great invertebrate phyla of Arthropodia and Annelida are notable for the presence of metamerism: a serial repetition of body parts in a long series of body segments. In annelids this segmentation is readily apparent; in arthropods the metameric structure may be more or less obscured in the adult, but is clearly seen in embryos or larvae.

Vertebrates, too, are segmented, but the segmentation is limited and has obviously developed independently from that of invertebrate groups, in which all structures, from skin inward to the gut, exhibit segmentation. Among the vertebrates neither skin nor gut is segmented; the metameric arrangement is primarily that of the trunk muscles. In relation, however, to the attachments of these muscles and their nerve supply, much of the skeleton and nervous system has taken on a segmental character.

The Body in Section (Fig. 2). We have noted some of the more important body features, with particular regard in many cases to their anteroposterior position in the body. We may now briefly consider the general organization of the body as seen in cross section.

Structurally, the most simple region of the body is that of the tail, strongly developed in most vertebrate groups. The section of a tail (Fig. 2, A, C) is typically a tall oval, the surface skin-covered. Somewhat above the center is seen the notochord, or the central region of the vertebrae which typically replace it in the adult, and, above this, a cross section of the nerve tube; the two structures are invariably closely associated topographically. The body cavity and associated viscera are absent in this region; representing them (in a sense) are caudal blood vessels lying helow the notochord. Almost all the remainder of the tail is occupied by musculature, usually powerful. This musculature is arrayed in right and left halves, with a median dividing septum above and below.

A typical section through the frunk is more complicated, even when, as in Figure 2, B, this is represented in its most generalized condition. One may consider the trunk as essentially a double tubular system, roughly comparable in structure to the casing and inner tube of an automobile tire. The outer tube in itself contains all the major elements seen in the section of the tail—motochord and nerve cord, and musculature descending on either side beneath an outer covering of skin. Internally, it is as if we had taken the little area below the notochord in the tail, where only the blood vessels were present, and expanded this to enormous proportions as the celomic cavity of the abdomen. With the development of this cavity the outer "tube" of the trunk now has an inner as well as an outer surface. The surface lining the body cavity is the peritoneum, and that part of this lining which forms the inner surface of the outer tube is the partical peritoneum. The part of the outer tube between celomic cavity and the surface of the body is the body wall.

The "inner tube" is primarily the tube of the digestive tract. The outer lining, facing the celomic cavity, is peritoneum—risceral peritoneum. The inner lining is the epithelium lining the digestive tract. Between the two, analogous to the musculature in the body wall, are present smooth muscle and connective tissues. In the embryo the gut is connected with the "outer tube" both dorsally and ven-

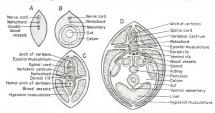


Fig. 2. Cross sections through the body of a vertebrate, A, B, Much simplified sections through tail and trunk, to show the essential structure of the trunk as a double tube; in the tall the "inner tube of the gpt is absent. C, B, More detailed diagrammatic sections of the tail and trunk to show the typical position of main structures.

trally by mesenteries—thin sheets of tissue bounded on either side by peritoneum. The dorsal mesentery—that above the gut—always persists, but the ventral portion frequently disappears for most of its length.

Although we shall treat of the arrangement of the organs in the celom in more detail in a later chapter, we may here go somewhat further in considering the position of the body viscera. (It must be noted that the relative size of the body cavity is never so great as represented in this and other diagrams; the viscera actually fill most of the available space.) In Figure 2, D, we have indicated the fact that the digestive tube is not a simple tubular structure, but has various outgrowths—most characteristically the liver ventrally and the pancreas dorsally. These are (in theory and in the embryo, at any rate) median structures, and are developed within the ventral and dorsal mesenteries. Further, we may have other organs projecting into the body cavity, but arising from tissues external to it. The kidneys in many groups project into the abdominal cavity at either upper lateral margin, and the reproductive organs—ovaries or testes—typically project into the cavity more medially along its upper border.

#### DIRECTIONS AND PLANES

Although the vertebrate body is essentially a bilaterally symmetric structure, there are many exceptions to this general statement. Organs which primitively lay in the midline may be displaced: the heart may be off center; the abdominal part of the gut—stomach and intestine—is usually twisted and the intestine may be convoluted in a complicated asymmetric fashion. Again, in paired structures those of the two sides may differ markedly; for example, in birds but one of the two ovaries (the left) is functional in the adult. A still greater asymmetry is seen in the flounders, where the whole shape of the body is affected by the substitution of the two sides for the normal top and bottom of the annial.

Either in theory or in practice the body of an animal may be sectioned in various ways at various angles. If the body is considered as sliced crossways, as one would cut a sausage, the plane of section is considered transverse. If the line of cleavage is vertical and lengthwise, from snout to tail, the plane is a sagitial one. Sometimes this latter term is restricted to a cut actually down the midline—the mediosagittal plane—and similar sections to one side or the other are termed parasagittal; but frequently such cuts are considered parts of a series of sagittal sections in a broad sense. The third major plane of cleavage, in the remaining direction, is that of slices cut the length of the body, but horizontally, each going through the width of the body. Such a plane is termed a frontal one—that is, one parallel to the "Forehead" of the animal.

Direction within the body is of importance in the description of structural relationships and the naming of the various organs. Terms in this category, fixing a position or pointing out a direction, may be considered.

The head and tail ends of the body are, in most vertebrates, the direction toward which and from which movement of the animal normally takes place. Anietior and posterior are the common terms of position in this regard; cranial and caudal are less used, but are essentially synonymous. Upper and lower surfaces—back and belly aspects—are reasonably named dorsal and ventral. Position in the transverse plane is of course given with reference to the midline; medial refers to a position toward the midline; lateral, a more removed position.

A fourth pair of terms of less positive meaning but of considerable use are proximal and disad. The former refers in general to the part of a structure closer to the center of the body or some important point of reference, the latter, to a part farther removed. These terms are clearly available to limb and tail structures. Within the head and trunk their use is less clear, but we may, for example, speak of proximal and distal parts of a nerve with obvious reference to the spinal cord or brain as a center, proximal and distal regions of arteries with reference to the heart as the assumed center, and so on.

For these adjectives of position there are, of course, corresponding adverbs ending in ly, and others (rather awkward) to denote motion in a given direction, ending in ad. as posteriorly, caudad.

The major directional terms, anterior, posterior, dorsal, and ventral, apply with perfect clarity to almost all known vertebrates. But in man we have an exception, an aberrant form which stands erect—and hence might have different directional terms applied to him.

It is unfortunate that in the terminology most generally used in medical anatomy this is the case (Fig. 3). The head and "tail" ends of the body are, in the erect human position, above and below rather than fore and aft, and are termed superior and inferior, rather than anterior and posterior. ("Cranial" and "caudal" could, of course, have been used instead, but medical people seem to like these alternatives no better than comparative anatomists.) More confusing, however, is the fact that anterior and posterior have generally been used in man -quite needlessly-to replace dorsal and ventral, so that the back side of the human body has been generally termed posterior and the belly surface anterior. Thus this pair of terms may have contradictory meanings in special human anatomy and in more normal usage, causing needless confusion. For example, each spinal nerve has two roots (cf. Fig. 364, p. 372). In a dissecting room the two roots in a human cadaver have been generally termed posterior and anterior. But if a neurologist working with (say) rats tries to use the same nomenclature, he is in an obviously absurd position; one root is no more "anterior" or "posterior" than the other. In both rat and man, however, designation of the nerve roots as dorsal and ventral is reasonable and logical. Long established customs, no matter how illogical, are hard to break down; but in a recently adapted revision of human anatomic nomenclature the use of dorsal and ventral has been agreed to in such cases.

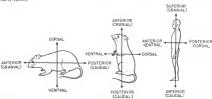


Fig. 3. Diagram to show the contrast in positional terms between normal vertebrates and man.

#### THE HOMOLOGY CONCEPT

Even in the early days of zoologic research it was recognized that within each major animal group there was a common basic pattern in the anatomic plan of the body. The same organs could be identified in many or all members of a group, although frequently much modified in size, form, or even function in correlation with changing habits or modes of existence. With the acceptance by biologists of the principle of evolution in the 60°s and 70°s of the last century, real significance was given to the concept of homology: the thesis that specific organs of living members of an animal group have descended, albeit with modification, slight or marked, from basically identical organs present in their common ancestor. For many decades the tracing out of homologies was a leading motif in zoologic research.

Many of the results of such studies were novel and exciting. It was found, for example, that the three little auditory ossicles of our own middle ear (p. 362) were in earlier days part of the jaw apparatus of our piscine ancestors, and appear still earlier to have been part of the supports of the gills of ancestral vertebrates. The muscles with which we smile or frown are derived from those which once helped our fish forebears to pump water through their gills.

Homologous organs are those which are identical—the same—in the series of forms studied. But what do we mean by "the same"? One tends, unthinkingly, to believe that the same actual mass of material, the very same limb or lung or bone, has been handed down, generation by generation, like an heirloom. This is quite absurd, but such a concept has obviously influenced, unconsciously, the minds of many workers. In reality, of course, every organ is re-created anew in every generation, and any identity between homologues is based upon the identity or similarity of the developmental processes which produce them.

The development of the science of genetics has given us a firm base for the interpretation of these processes. They are controlled by hereditary units, the genes. These tiny structures are present to the number of some thousands, at least, in every animal cell. The development of the individual is directed by the genes transmitted to the fertilized egg by the parents. Each gene may affect the development of a number of structures or parts of a body; conversely, every organ is influenced in its development by a considerable number of genes. If the genes remain unchanged (paper from generation to generation, the organ produced will remain unchanged (apart from transient environmental effects upon an individual), and the homology is absolute.

ual), and the homology is absolute.

Changes, however, do occur in genes, as mutations; these mutations produce changes in the structures to which the genes give rise. If the mutations produce effects of small magnitude and occur in only a few of the genes concerned, the organ will be little modified, and its homology with the parent type will remain obvious. If, however, the mutations are numerous and marked in their effects, the organ may be radically modified and its pedigree much less clear. In a sense, a study of organ homology is merely a study of phenomena produced by genes. If the genetic constitution of all animal types were well known, the determination of homology between structures might well rest upon the degree of identity of the genes concerned in their production. But this is not a matter of practical import, for there are few animals whose genetic constitution is adequately known, and it is improbable that our range of knowledge will ever be broadened to the necessary degree.

What are the best criteria for the establishment of homology? Function is no sure guide, for organs which are clearly homologous in two animals may be put to quite different uses. Observation shows that the shape, size, or color of a structure gives little positive evidence of identity. Similarity in general anatomic position and relations to adjacent organs is a more useful clue to identification. Best of all is similarity in developmental history. Embryologic processes in vertebrates tend to be conservative, and organs which are quite different in the adult condition may reveal their homology through similarity in early embryonic stages.

Homology is generally applied to structural identity. Some have proposed that the concept be broadened to include functional identity. This suggestion has not, however, met with general acceptance. The term analogy is in some regards a parallel, on the functional side, to homology, analogous organs are those which have similar functions. It is, however, somewhat restricted, for as generally used it implies that the organs concerned are not homologous. A lung and a fish gill, for example, are analogous, for both are used for respiration, but the two are quite different structures.

#### ADAPTATION AND EVOLUTION

The varied modifications which vertebrate structures have undergone and the varied functions which they have assumed have, of course, come about as the result of evolution. One cannot make a comparative study of the vertebrates without formulating some general concept of the nature of evolutionary processes. Most structural and functional changes in the vertebrate body are quite clearly adaptive modifications to a variety of environments and modes of life. How have these adaptations been brought about? Proper discussion would require a volume in itself; we can here merely indicate the general nature of the problems concerned, and current majority opinion as to their interpretation.

We sometimes speak, thoughtlessly, of adaptation changes, as if the animal "willed" them or as if its needs or desires in themselves brought new structures or structural changes into being. It would be advantageous, one might say, for a fish to be able to walk on land, and so some fishes made themselves legs; it would be "nice" if the cow's early ancestors developed teeth better able to cope with grain and grass, and so the teeth promptly deepened.

Ohviously, such ideas are alsurd. They are, however, not far removed from certain theories of evolution which have had, and still have, a certain vogue. These assume that evolution is an unnatural phenomenon; that changes have been brought about by some "inner urge" within the organism, or are the result of the 'design' of some supernatural force. Since such theories are nonscientific, they cannot be scientifically disproved; but we are at liberty to look for more reasonable explanations of evolution, based on known facts. If someone tells me that the operation of my automobile engine is controlled by an invisible demon dwelling therein, I cannot prove him wrong. But nothing is gained by adding this hypothetic demon, and I would prefer an attempt to explain the engine's working in terms of known mechanical principles, the nature of electric currents, and the explosive structure of hydrocarbon molecules.

A more plausible attempt at interpretation of structural evolutionary changes was that first advocated over a century ago by Lamarck—a belief in the inheritance of acquired characters through the effect of use and disuse. If the giraffe's

ancestors stretched their necks after foliage on high branches, the effects of stretching, this theory assumes, would be transmitted to their offspring, generation after generation, and an elongate neck gradually developed in the hereditary pattern. If the snake's lizard ancestors ceased to use their legs in locomotion, the cumulative result of disuse would be the eventual loss of the limbs. This attractive theory seems simple, reasonable, and natural. But its present standing is poor indeed. We may summarize by saying that no one, despite repeated efforts, has been able to furnish any valid proof of any instance of the inheritance of an acquired characteristic. Structures useful to an animal may and often do increase in size or complexity in the course of time, and useless or little-used structures may diminish. But there is not the slightest evidence that the use or disuse of parts by an individual has any effect whatever upon the build of its offspring.

The science of genetics has in recent decades demonstrated that evolutionary changes are due to mutations. These may produce effects of some magnitude, but most cause only minor modifications: a mutation in a fruit fly may, for example, have no greater visible result than the splitting of a single briste. We do not fly understand the various ways in which mutations are caused, although we are currently beginning to gain an idea of the chemical structure of the materials involved, and of chemical and physical influences (such as radiation) which play important roles in bringing them about. As for evolutionary theories, however, two things stand out clearly (1) There is no evidence of 'design' or 'direction' in mutations. They appear to be quite random, rather than tending in any one direction. Some may well be advantageous; most, however, are obviously harmful, and many are lethal. (2) There is no evidence that mutations have any relation whatever to use or disuse of hody organs; characters acquired by the individual have no specific influence on the nature of mutations of the genes in its sex cells—mutations whose effect is transmitted to the offsoring.

The process of mutation thus seems to be merely one of blind, random change. But vertebrate evolution certainly appears to have resulted in changes both useful and adaptive. How can such results have come out of the mutation process?

Part, at least, of the answer was given by Darwin nearly a century ago. He was, of course, quite ignorant of the data now available from genetics, but reasonably assumed that there existed some hereditary mechanisms of the sort with which we are now familiar. Given a supply of random mutations, natural selection will act powerfully to eliminate unfit types and preserve the better-fitted forms in which one or a group of useful mutations have occurred in the germ plasm. Even the slowest breeders among animals produce more individuals than can survive. Many are destined to die before becoming adults and reproducing—an act which is nature's standard of success. Which individuals are eliminated is partly a matter of chance. But both observation and experiment indicate that even small mutations in an adaptive direction have a distinct survival value and may become dominant in a species in a short time. This natural selection of such a random series of mutations as have adaptive value would appear to be a major mechanism of evolutionary change.

Evolution, however, is a much more complicated process than a mere adaptive selection of features developed in a given individual. We may note, for example, the fact that in general genes are carried in duplicate in the cells of every animal (one gene coming from each parent); if the members of a gene pair differ in their potentialities, one tends to dominate over the other in the structures or functions which it controls. It is obvious that selection can have no influence over the "weaker" of such a pair of genes—technically termed recessive—unless by chance both members of the pair of genes concerned are of the same recessive nature. A little consideration makes it clear that as a result of this situation it is practically impossible to eliminate completely a recessive mutant, even if highly deleterious, from an animal stock in which it is once established. It is reasonable to believe that with numerous variables of this sort present in a stock, circumstances might arise tparticularly in changed environments) in which certain "suppressed" variants or combinations of them might eventually prove highly savia tageous if they should come to light in an individual and result in evolutionary change in the population as a whole.

#### SURFACE-VOLUME RELATIONS

It is frequently seen that in any group of animals large and small forms differ notably in the relative size of various organs or parts. The reason for many of these proportionate differences lies in a geometric principle so obvious that it is generally overlooked, namely, the fact that as the size of an animal (or any other object) changes, surfaces increase (or occrease) proportionately to the square of linear dimensions, while volumes change proportionately to the cube of linear dimensions.

This principle is of wide application, for surface-volume relationships are to be found in a variety of structural and functional features of vertebrates. We cite obvious examples: (1) The strength of a leg (like any supporting column) is proportional to its cross section, which varies as the square of linear dimensions, whereas the weight which it supports is proportionate to the cube of linear dimensions. In consequence an elephant cannot have gazelle-like legs. (2) The amount of food which an active animal needs is roughly proportionate to its volume.\* the amount of foodstuffs which its intestine can absorb depends upon the area of the intestinal lining. In consequence, large animals have a disproportionately clongated intestine or one with a complicated structure, resulting in a greater internal surface area for digestion.

#### NOMENCLATURE

The student of vertebrate morphology is confronted with a bewildering array of unfamiliar names of anatomic structures. This is unfortunate but inescapable. Vertebrate structures are numerous, for many there are no every-day terms. Even where such names are available, they are often vague and not exactly defined in common usage. Further, it is desirable to have some international system of terms understood in the same sense by scientists of every country.

When anatomy was first studied, all "learned" works were, as a matter of course, written entirely in Latin. In consequence, Latin names where already in existence were applied to anatomic structures, and if no term existed, one was manufactured from Greek or Latin roots and cast in Latin form. Some notes regarding the formation of anatomic terms are given in Apoendix II. Today Latin

<sup>\*</sup> Emphasis on active; basal metabolism in a resting condition is quite another thing.

has cassed to be an international language as far as the general text of scientific books is concerned. Latin anatomic terms, however, are still in vogue. We cannot do without them, although we often use them in a somewhat "anglicized" form speaking, for example, of the "deltoid musele" of the shoulder rather than the "museulus deltoideus," or of the "parietal bone" rather than the "os parietalis."

Latin is, of course, an inflected language, and its nouns and adjectives have a variety of endings to express not merely singular and plural numbers, but also a variety of cases and a rather arbitrary system of genders. Until recent decades some knowledge of Latin grammar was part of the equipment of every college student, and the manipulation of Latin terminology presented no difficulty. Today this is not the case; rather unfortunately, for a biologist should at least know enough to avoid such gaucheries as speaking of "humeruses" instead of humeri, "femurs" instead of femora. Fortunately the number of noun and adjective endings ordinarily used in anatomic terms is limited, and these can be readily learned.

It is accepted procedure in anatomic nomenclature that where a structure is present in mammals-particularly in man-the name there used be applied to the same structure in other forms. Thus, for example, man and many mammals have a clavicle, or collar bone, and the equivalent element in the shoulder structure should be called by the same name in reptiles, amphibians, or fishes, even though its appearance is radically different. Sometimes, however, too hasty an identification may be made and a name wrongly applied. Teleost fishes have a bone similar in position to the clavicle, and that name was customarily given to it; we now know, however, that the teleosts have lost the true clavicle; the bone present there is a different one (the cleithrum, p. 154). If homologies are in doubt, it is better to use a different name for the structure in question. For example, there is a muscle in the thigh of reptiles which may be homologous with the sartorius muscle of mammals; but since there is some doubt of the homology, it is customary to give the reptilian muscle a different name—the ambiens muscle (p. 215). If a structure encountered in a lower group has no mammalian equivalent, a new name must, of course, be coined.

Although anatomic terminology has been in general a rather stable and uniform system, there arose, quite naturally, a number of differences in terminology between different schools of work and in different countries. Motivated by the laudable desire to achieve uniformity, the German anatomic association, in convention at Basel some decades ago, brought forward a comprehensive scheme of terms which they hoped would receive universal adoption in human anatomy. This terminology, usually referred to as the "BNA," was adopted by medical schools and has been widely used in medical work. Quite a number of the terms in this terms of body position. At an international congress of anatomists in Paris in terms of body position. At an international congress of anatomists in Paris in 1955 a modified code was drawn up, improving the situation to a considerable degree, and the revisions embodied in the new "PNA" are now gradually supplanting the older terms in medical school practice.

# 2

## THE VERTEBRATE PEDIGREE

Although the present work primarily concerns the vertebrates alone, we must recognize that there exist various animal types lacking a backbone, but closely allied to the vertebrates. Study of these more lowly forms contributes to our understanding of vertebrate structure and history. Further, although (as will be seen) we have little certain knowledge of the early ancestry of the vertebrates, the subject of their pedigree deserves consideration. In this chapter we will first describe, as lower chordates, certain small marine animals definitely allied in some fashion to the vertebrates, then discuss possible relationships of the vertebrates to various invertebrate phyla, and, finally, attempt to plot out a reasonable vertebrate pedigree.

The vertebrates do not in themselves constitute a major division of the animal kingdom. They are considered merely one subdivision—although by far the largest subdivision—of the phylum Chordata, the other members of which are to be considered briefly here. The "lower chordates" lack the backbone and many other advanced structures of their vertebrate relatives. They do, however, exhibit, to a variable degree, basic features characteristic of the vertebrates and not found elsewhere in the animal kingdom. These features indicate that they are ruly related to vertebrates and hence properly included in a common group with them. The term Chordata itself implies that a notochord (or chorda), or some structure thought to be equivalent to a notochord, is generally present. Again, a dorsal nerve cord is a common feature. Most characteristic of all is the fact that gill slits are almost universally present in chordates.

Amphioxus. 'By many workers the phylum Chordata is subdivided into four subphyla—in roughly ascending order, Hemichordata, Uncehordata, Cephalochordata, and Vertebrata. Here we reverse the order and begin our discussion of the lower chordates with the Cephalochordata, in which the similarities to the vertebrates are most obvious. The subphylum includes only a few closely related forms, all commonly termed Amphioxus (Figs. 4, 5). They are translucent amials, fishlike in appearance and proportions, found in shallow marine waters in

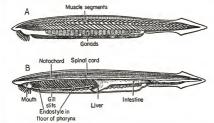


Fig. 4. Amphioxus, a primitive chordate. A, As seen through the transparent skin; B, a sagittal section. (After Gregory.)

various regions of the world, and sometimes locally abundant. As the shape suggests, they can swim readily, but because of poor development of fins, rather ineffectively; for the most part they spend their time with the body buried in the sands of the bottom, with merely the anterior end projecting.

Despite the piscine appearance, it is obvious that we are dealing with forms far more primitive than any fish. There are no paired fins or limbs of any sort. Cartilage-like materials stiffen the gills, dorsal fin, and mouth parts, but no part of the normal vertebrate skeleton of vertebrac, ribs, or skull is to be found. The main skeletal structure (apart from connective tissues) is a highly developed noto-chord, which persists through life and (in contrast to the vertebrates) extends clear to the tip of the "nose"—a feature to which the group owes its name. The noto-chord prevents telescoping during vigorous swimming and serves as a convenient central "peg" on which to hang the body organs. There are nerves serially arranged along a typical, dorsal, hollow nerve cord; but although the cord is somewhat larger anteriorly, there is no true brain, and there are only dubious traces of sense organs which might correspond to nose or eye. Much as in fishes the major musculature consists of a segmental series of muscle blocks arranged in Vs down either side of the body; alternating waves of contraction of these muscles bring about the swimming movements.

For the most part the digestive tract is of a very simple nature. There is a mouth eavity (buccal carity) surrounded by a circle of stiffened projecting is a The pharynx is greatly clongated, extending about half the total length of the body. Back of the pharynx, the gut is a straightforward tube with little sign of division into successive chambers, although chemical treatment of food appears to predominate in the anterior part of its length, absorption at the back. There is a large pouchlike outgrowth which is generally compared to a liver although the homology is dubious. As in vertebrates, the tube ends at the anus, far short of the end of the body, which thus terminates in a true tail.

The pharynx is highly specialized for food collecting. Amphioxus lives on particles gathered from the sea water; these are taken in through the mouth by

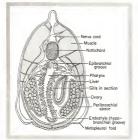


Fig. 5. Cross section of Amphicus though the playrays. The pribrenchial space surrounding the pharyas, liver, and so on, is, desplie is seeming internal position, actually external to the body and is somewhat analogous to the gill chamber of bony fishes, and the like. It is formed bony fashes, and the like, it is formed bony fashes, and under the playray of great folds meeting one another ventrally, and it folds meeting one another ventrally, and it is a formed position of the proposition of the propos

ciliary action and strained out from the water as it passes out of the body through the gill slits. These slits are very numerous, far more so than in any vertebrate, for there may be as many as fifty or more pairs of them, and each gill is essentially a double structure, developing in much the horseshoe-shaped fashion seen in acorn worms (Fig. 9). A peculiar hood grows downward and encloses the whole gill system, serving as a protection to these delicate organs when Amphioxus is buried in the sand, and forms a pocket, the atrium, opening to the surface only by a pore at the back of the pharynx. But while the gill slits, by their major development, emphasize the animal's relationships to the vertebrates, they differ from the typical vertebrate gill apparatus in both purpose and mode of operation. It appears that much of the "breathing" of Amphioxus is done through the skinwhich, in contrast to that of vertebrates, is quite thin-and that here, as we shall see in other lower chordates, the gills are primarily feeding devices. Further, water currents through the gills in vertebrates are effected by muscular pumping; in Amphioxus ciliary action alone is responsible, and cilia are highly developed in the pharynx. A prominent feature is the development of a longitudinal midventral (hypobranchial) groove termed the endostyle, running the length of the pharynx; in this a sticky mucus is abundantly secreted. Ciliary currents carry streamers of this material up the pharynx walls, past the gill slits; catching up trapped food particles on the way, the mucus collects in a dorsal (epibranchial) groove. From this point cilia carry back the mucus and the enclosed food particles in a continuous slimy band to the intestine; the animal feeds itself by a conveyor-belt system.

The major blood vessels of Amphioxus are laid out clearly on the vertebrate pattern (Fig. 305), with the blood coursing forward ventrally and back dorsally after passing upward through the gill region. There are, however, no blood cells, red or white, or blood pigments and, further, there is no heart; movement of the blood is accomplished by wave contraction of some of the principal vessels, to gether with the contraction of numerous tiny heartlike bulbs situated along the course of the atteries below the gill region. The gonads differ from those of vertebrates—indeed, from those of all other chordates—in being numerous and segmentally arranged. Still more divergent from the vertebrate plan is the nature of the exerctory organs. The vertebrate kidney is of a unique type, composed of distinctive water-filtering units which will be described in detail later. In Amphioxus, on the other hand, the structures are of a very different sort; they are, as in invitebrates generally, segmentally arranged nephridia, which in Amphioxus resemble to a degree those characteristic of many annelid worms.

Where does Amphioxus stand in relation to the vertebrates? A few theorists, for whose ideas as to vertebrate evolution the existence of Amphioxus is inconvenient, deny that it is related. But the features in which Amphioxus resembles the backboned animal are so numerous and so basic that this position is untenable. Strongly in contrast is the suggestion that Amphioxus is a degenerate vertebrate. As we shall see, the young of lampreys, quite unlike the adults, live a life as sedentary filter-feeders and are comparable to Amphioxus in many ways. Is Amphioxus a lamprey which has, so to speak, never grown up and hence retained, as an adult, the simplicity of structure of the larva? It is probable, as we shall see presently, that the phenomenon known as neoteny, in which a larva lingers long in a youthful state before finally changing into an adult, and the more extreme condition of paedogenesis in which it becomes sexually mature without ever reaching the adult condition, are factors to be kept in mind in studies of evolutionary lines. But Amphioxus shows many features which are not merely more primitive but different from those expected in the young of a lamprey ancestor-too many to make this suggestion of relationship by degeneration plausible. As a working hypothesis we shall here, like a majority of students of the subject, interpret Amphioxus as a somewhat specialized survivor of a type of animal ancestral to the vertebrates. As will be seen later, it is important to realize that Amphioxus is not only more primitive structurally than any vertebrate, but has a mode of life essentially different from and more primitive than that of vertebrates. In general vertebrates actively and aggressively seek large food objects, eat by muscular movements of jaws or analogous structures and typically use their gills-operated by means of well-developed muscles-exclusively for breathing purposes. It is often tacitly assumed that the vertebrate ancestor was likewise a vigorous, active swimming form. But Amphioxus, although able to swim, is essentially sedentary and, as we have noted, is in contrast a filter-feeder, using cilia rather than muscles in food gathering and utilizing the gills for feeding rather than breathing.

Tunicates (Figs. 6–8). In seeking further lowly relatives of the verteenters we may be well advised to look for other filter-feeders which, even if more simple in structure than Amphioxus, show at least some of the basic chordate characters, such as gill slits, notochord or nerve cord. Such a group is that of the Corchordata, the tunicates or sea squirts and their relatives. These are rather common small marine organisms. They are essentially inactive; the adult does not seek its food, but is a highly developed filter-feeder, accepting such particles as it can attract by ciliary action. Many tunicates are found floating freely in the water, singly or in groups, often as into barrel-shaped structures; others are attached to the bottom, either as branching colonies or as individuals (Fig. 8, CB). Simplest are the solitary tunicates (Fig. 6, B). As an adult, such an animal is an almost formless lump attached to a rock or other underwater object and covered with a leathery-looking "tunic." The only structural features seen externally are an opening at the top, into which water passes, and another, lateral, opening,

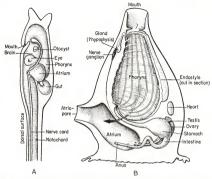


Fig. 6. A solitary unicate. A. Diagram of the structures seen in the free-swimming larva (based end above, and only a short section of tail figured). The otocyst is a simple car structure. B. The essilie adult, formed by elaboration of the structures at the anterior end of the larval body. The original dorsal side lies at the left. The large plarynx is attached to the body wall above and below (left and right in the figure); the artium (corresponding to the perharantial space of Amphisoxa) bounds it on either side. Water passing through the latticework gills of the pharynx enters the atrium and, as indicated by the arrow, streams out through the atripopore. (After Delagae and Herouard.)

through which the water current flows outward. The creature shows no external resemblances to the vertebrates, and internally much of the structure is equally unfamiliar to a student of that group. There is no notochord. Nor is there a nerve cord; instead, there is a simple nerve ganglion with a few nerves splaying out from it.

Much of the interior of the animal is occupied by a barrel-shaped structure which serves as the food-gathering device. The water current, entering it through ciliary action, is strained through slits in the sides of the barrel into a surrounding chamber, the atrium, which leads to the lateral excurrent opening. On closer examination it becomes obvious that the barrel is an exaggerated set of internal gills, constituting the pharyngeal region of the animal; there is even an endostyle comparable to that noted in Amphioxus. Behind the enormous pharyns, the digestive tube narrows to forme sophagus, stomach, and intestine—all of modest size.

We have here, in the pharyngeal gill apparatus, a high degree of development of one of the primary characters to be sought in a relative of the vertebrates. For other chordate characters, however, we must turn to the developmental history. In many tunicates propagation takes place in the main by a procso of budding. But in some there is a distinct larval form (Figs. 6, 4, 7), which

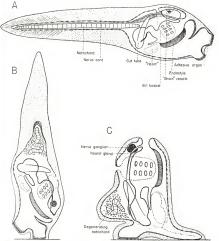


Fig. 7. Metamorphosis of a solitary tunicate. A, The free-swimming larva (cf. Fig. 6, A). B, The larva has attached itself to the bottom, and tail degeneration is under way. C, Except for remains of the notechord, the "somatic" structures have disappeared, and the build is close to that of the degenerate adult. (After Davydoff.)

has rather the appearance of an amphibian tadpole (in one small group of tunicates the larval form persists in the sexually mature state). The "head" of the larva corresponds to the entire body of the adult. The tail is a swimming organ, useful in transporting the young tunicate about in its search for a home. Once the animal attaches and "settles down" to its sedentary adult existence, the tail dwindles and is absorbed into the body. In this tail, however, are to be found major proofs of vertebrate relationship of the tunicates. There is in the larval tail (as the group name implies) a well-developed notochord and, above this, a typical hollow dorsal nerve cord. These tail structures are, however, less advanced than those of Amphioxus, for there is here no segmentation of the swimming muscles or of the nerves supplying them. Anteriorly, there are in the larva a rudi-mentary brain and sense organs. At metamorphosis, the notochord and the larval nerve cord (unnecessary in the sessile adult) disappear.

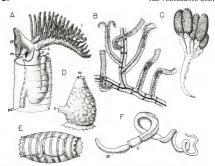


Fig. 8. Tunicates and hemichordates. A. An individual of the pterobranch grous Rhabdoplevar projecting from its enclosing tuke. B. A part of a colony of the same. C. A colonial sessile tunicate; each polygonal area is a separate individual of the colony. B. External view of a solitary tunicate (cf. Fig. 6, B). E. A free-floating tunicate, or salp. F. An acron worm (Balanoglossus), a. Amus.; c, ollar groun, i. Daphophore, m. mouthe, p. pero or opening from colonic pd. stalk (perducel by which individual is attached to remainder of colony; ps. probosics or anterior projection of body; κ, siphon which carries off water and body products. (Mainly after Delage and Herount.)

The tunicates, thus, are definitely chordates and definitely related to the vertebrates. How do they fit into the evolutionary story? Those who believe that the vertebrate ancestors were from the earliest times actively swimming animals would regard the tunicates as a degenerate side branch of the vertebrate ancestral line and consider that the common ancestor of vertebrates and tunicates was as an adult a free-swimming form, somewhat like the larval tunicate. From this, it is suggested, the vertebrates "ascended" by an improved continuation of an active mode of life, whereas the tunicates tended to become degenerate and lost most progressive structural features except for the food-straining gill barrel; became, in fact, fit subjects for evolutionary sermons on the results of slothful living. There is, however, another interpretation which one may consider; namely, that the chordate ancestor of the vertebrates was, rather, a sessile food strainer somewhat like an adult tunicate; that the tail first appeared as an adaptation in the larva, rendering easier the search for a suitable place in which the animal could "settle down"; and that the development of higher forms came about by the retention of the tail and the free-swimming habit in adult life with the elimination of a sessile adult stage.

Acorn Worms. The third group of forms definitely related to the vertebrates is that of the Hemichordata. Here the key chordate characters are little developed, and many writers would erect the hemichordates into a phylum separate from the Chordata, although related to them.

The best known hemichordates are the acorn worms, such as Balanoglossus (Figs. 8, 9), termed as a group the Enteropneusta and found not uncommonly in tidal flats. The long, slender body suggests that the acorn worms are active animals, as one might hope for in vertebrate ancestors. This is not the case; they are essentially sedentary mud burrowers and are filter-feeders comparable in their general mode of life to the tunicates. The general body shape is wormlike, but there the resemblance ends, for their structure is not at all comparable to that of ordinary annelid worms. Even externally the acorn worms are distinctive. The body terminates anteriorly in a tough yet flexible and muscular "snout" or proboscis, of variable length, which serves as a burrowing organ. Behind the proboscis there is a distinct thickened section of the body, the "collar" region; the name acorn worm is due to the fact that in some forms the proboscis and collar have the appearance of an acorn in its cup.

In most regards the acorn worm shows no especial resemblance to the vertebrates or other chordates. For a short distance-in the collar region-there is a dorsal nerve cord which is more or less hollow. But over the rest of the body the nerve cells and fibers are rather diffusely distributed in the skin, although there is some development of solid dorsal and ventral strands of nerve tissue. There is no proper notochord, although a stout pouch of tissue at the base of the proboscis has been compared (rather dubiously) to an imperfectly developed structure of that sort.

But-as in tunicates-we find that a vertebrate type of gill system is present in characteristic and highly developed fashion. The gills are not so pronounced as they are in tunicates, but there is, behind the collar, an extended pharynx (partitioned off from the food passage to the stomach), from which on either side open out gill slits quite comparable - even in details of structure and development-to those of Amphioxus. Vertebrates are surely not descended from acorn worms as such, but these forms may reasonably be interpreted as a group not distantly removed from our early chordate ancestors-essentially sedentary food-

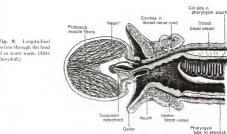


Fig. 9. Longitudinal section through the head of an acorn worm. (After Dawydoff.)

strainers in which, however, some degree of potential motility is present in the adult.

The acorn worms show, in the gill slits at least, definite proof of vertebrate relationships. But in a second type of hemichordates, the Pterobranchia (Fig. 8, A, B), hardly a trace of vertebrate structure is to be found, and were it not clear that they are affiliated with the enteropneusts, one would hardly suspect that they belonged to this general stock. The pterobranchs are tiny, rare marine animals of which only a few genera are known. They form little plantlike colonies, whose individuals project like small flowers at the ends of a branching series of tubes, The short body is doubled back on itself, so that the anus opens anteriorly back of the head. Proofs of relationship to the acorn worms lie in the fact that there is a snoutlike anterior projection beyond the mouth, corresponding to the enteropneust proboscis, and back of this a short collar region. But other resemblances to acorn worms-to say nothing of more highly developed chordates-are almost lacking. There is little development of a nervous system, no trace of a hollow nerve cord, and not the slightest suggestion of a notochord. And the feeding mechanisms are of a very different type. True, these plantlike animals feed, as do more typical lower chordates, on food particles drawn in by ciliary action. But the gill mechanism, which is so important in the filter-feeding of acorn worms. tunicates and Amphioxus, is almost absent. One of the pterobranchs has a single pair of small gill openings, the others none at all. Instead, there project from the collar region large tentacle-like structures, termed lophophores; these are supplied with bands of cilia which collect food particles and bring them to the mouth.

So unchordatelike are these small creatures that one is tempted to suggest that they are degenerate, perhaps relatively modern in development. But it has recently been suggested that they are a very ancient group indeed. Paleontologists have long been familiar with a variety of small tubelike structures termed groupolities which were abundant in the seas far before the appearance of the oldest vertebrates. It is claimed that these tubes are similar to those which shield the modern pterobranchs.

With the pterobranchs we conclude the series of lowly chordates. \*What do they teach us as to vertebrate origins? The answer is far from clear. As we have said, one (at first thought) would hopefully expect the ancestral line to lead through active little forms, paralleling, at least, such invertebrate groups as the various worm phyla and the progressive arthropods such as crustaceans and insects. But consideration of the lower chordates tends to dim such expectations. For the most part we see sluggish and sedentary habits, and instead of forms actively searching for food, passive filter-feeders. But before attempting to reach a conclusion let us survey the various invertebrate phyla in search of possible chordate relatives.

Invertebrate Phylogeny. In recent decades students of invertebrate zoology have tended to agree on a fairly uniform scheme of phylogeny of the major groups of animals without backbone (Fig. 10). The coelenterates for Cni-daria, as some authorities term the group) including such forms as jellyfishes, sea anemones, and corals may lie close to the basal stock of metazoans—all animals, that is, above the level of protozoans and sponges. The coelenterates have

<sup>\*</sup> Possibly allied to chordates also are some tiny, deep sea forms termed the Pogonophora; but they are poorly known, and obviously degenerate, and we may leave them, without loss, in oblivion.

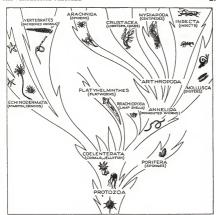


Fig. 10. A simplified family tree of the animal kingdom, to show the probable relationships of the vertebrates. (After Romer, Man and the Vertebrates, University of Chicago Press.)

a simple, two-layered structure, with little between the "skin"—the ectoderm and the lining, termed the endoderm, of the inner gut cavity. Above the coelenterate level most animals have a third intermediate body layer, the mesoderm, from which muscular, circulatory, and other systems are formed; the mesoderm becomes—in bulk, at any rate—the most important of the three tissues. Further, many invertebrates develop a celom within the mesodermal tissues.

Two contrasting methods of embryonic formation of this third body layer are to be seen. In one type especially characteristic of echinoderms—starfishes, sea urchins, sea lilies and the like—the mesoderm arises in the form of pouches growing outward from the gut walls; these pouches remain in the adult as closed body cavities. In a second type the mesoderm arises as solid masses of cells budded off from an area near the posterior end of the body, and the body cavities, when formed, arise by cleavage within the masses of mesodermal cells. To this second type belong the annelid worms and the molluses. The great group of jointed-legged animals, the arthropods, appear to belong to this second group as well. although their developmental pattern is much modified; and certain other forms, such as the flat worms, appear to be offshoots from the base of this major stock. We thus have the concept that, above the coelenteral level, the inverte-

brates form two great branches, in Y-fashion, with the echinoderms at the end of one branch and the great host of familiar advanced invertebrates clustered on the other. A few of the less familiar sessile marine forms, such as the lamp shells (brachiopods) and moss animalcules (bryozoans), do not fit well on either main branch but are perhaps somewhat closer to the echinoderms.

The two stocks contrast not only in the type of formation of the middle body layer, but also in the larval development. Both echinoderms on the one hand and water-dwelling annelids and molluses on the other grow from the egg into tiny larvae of simple structure, with bands and tufts of cilia arranged in characteristic patterns on the surface of the body. The echinoderm larva has an arrangement of the ciliated bands and other features which differ markedly from those of the larvae of annelid worms and molluses.

From what point on this family tree of the invertebrates does the chordate (and vertebrate) branch arise? Theories on this subject have been numerous, but have given few positive results.

One solution to the problem might be to suggest a direct origin of chordates from the most primitive metazona son the coelenterate level. Here there are no great difficulties to overcome, for animals on this level of evolution have few specialized features which must be lost before starting on the path toward the vertebrates. But in reality, advocacy of coelenterate descent would seem to be begging the question. A number of basic advances not made by the coelenterates are found in almost all other invertebrate phyla—development of a middle body layer, presence of both mouth and anus in the digestive tract, and so forth. It seems highly improbable that the vertebrates acquired these progressive features entirely independently of other groups. Search seems warranted for possible relatives—if not direct ancestors—on a higher level.

Annelids as Ancestors. The annelid worms offer a possible point of departure; the theory of vertebrate origin from annelids was warmly advocated during later decades of the nineteenth century. The lowly angleworm is none too prepossessing as an ancestor; but there are numerous marine annelids of a more progressive and attractive nature. Annelids have a typical bilateral symmetry, as do vertebrates, and, in correlation with this, some are, like typical vertebrates, active animals in contrast with the sessile types common in many invertebrate phyla. Then too, they are segmented forms, as the vertebrates are to at least some extent. As in vertebrates, the central nervous system is composed of a brainlike mass at the anterior end of the body and a longitudinal nerve cord.

So far, so good. But beyond this point the comparison breaks down. Even the segmentation is not a perfect argument; for the anneld is segmented in every respect, from skin to gut lining, whereas the segmentation of a vertebrate is primarily confined to part of the middle body layer. The annelid has, it is true, a longitudinal nerver cord. But it is solid, not hollow, and it is ventral rather than dorsal in position. This last point is especially troublesome to advocates of this theory. They have "resolved" the difficulties by assuming that a vertebrate is a worm upside down (Fig. 11). This is hard to swallow (even a worm may have some idea of which way is up) and involves further perplexities. The worm mouth is on the under side of the head, and so is that of a vertebrate. A reversal of surfaces implies that the old mouth of the worm has closed and been replaced, historically, by a new one. Attempts have been made to find traces of the theoretic old mouth opening in vertebrate embryos—it should pass upward and forward through the brain to the top of the head!—but without convincing results.

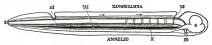


Fig. 11. Diagram to illustrate the supposed transformation of an annelid worm into a vertebrate. In normal position this represents the annelid with a "brain" (s) at the front end and a nerve cord (x) running along the underside of the body. The mouth (an) is on the underside of the animal, the anus (a) at the end of the tail; the blood stream (indicated by arrows) flows forward on the upper side of the body, back on the underside. Turn the book useide down

and now we have the vestebrate, with nerve cord and blood streams revereed. But it is necessary to build a new mouth (s) and sume (pv) and close the old one; the vorm really had no notochord (w); and the supposed change is not as simple as it seems. (From Wilder, History of the Human Body, by permission of Henry Holt & Co., publishers,

Even if this difficulty in orientation be solved, there are more ahead. There is no trace in an annelid of a notochord or of internal gills. This may be discounted, perhaps, by the fact that (as we have seen) these structures are little developed in some of the simplest chordates. But a crucial difference is that the type of mesoderm formation is in contrast, for in chordates the pouch type of mesoderm formation is the basic pattern. There is, thus, almost no positive reason to believe in a descent of vertherates from annelids; and there are so many difficulties in the way that there is today little reason to take stock in an annelid theory.

Arachnids as Ancestors. The arthropods, including crustaceans, myriapods, arachnids, and insects, are, it is agreed, descended from annelids or from worm ancestors closely related to them. The arthropods include the most progressive and successful of all invertebrate animals, and it is not unnatural that they have received considerable attention as possible vertebrate ancestors. Among the arthropods it is the arachnids that have been selected as the most likely candidates for vertebrate kinship. Spiders are the commonest of arachnids, but the scorpions are more generalized types. Still more primitive are aquatic arachnids, including the horseshoe crab (Limius) and relatives of high geological antiquity, one ancient extinct group, the eurypterids, has been thought by some to be close to the ancestry of the vertebrates.

In arachnids, as in annelids, there is a ventral nerve cord. This gives us the same problem that was encountered in the worms: the upper and lower surfaces must, it seems, be reversed, a new mouth exchanged for an old one, and so on, Again as in annelids we find conspicuous differences from vertebrates in segmentation; still again, there is no trace in arachnids of notochord or internal gills. An added difficulty with arachnide as an enestors of the vertebrates is the presence of unmerous, complex jointed legs of arthropod character. It is impossible that these were transformed into fish fins, and the arthropod legs must be done sawy with before the development of vertebrate appendages can begin. The old eurypterisk were covered with chitinous armor, which in some cases had a superficial resemblance to the bony armor of certain archaic fishes, such as those shown in Figure 18. But even this resemblance is meaningless; for the resemblance is a top-to-top one, whereas, because of the reversal of surfaces; it should be the bot-

tom of the arachnid which resembles the upper side of the vertebrate. To sum up, to make a backboned animal out of an arachnid, the supposed ancestor must have lost almost every characteristic feature he once possessed and reduced himself practically to an amorphous jelly before resurrecting himself as a vertebrate.

An amusing variant of the arachnid theory removes a whole series of difficulties caused by the necessity of turning the arachnid over to make a vertebrate. Under this theory there has been no reversal of surfaces. It is pointed out that the arthropod digestive tube has expansions and subdivisions which rather resemble the cavities of the brain and spinal cord of vertebrates. This particular theory assumes that the original ventral nerve cord of arachnids migrated upward to surround the original digestive tube, which actually became the cavities of the nervous assistem; and that meanwhile a brand new digestive tract developed by a closing over of the furrous present ventrally between the jointed legs. Technically, this theory solves the difficulties encountered in turning the animal over, but it appears to offer fresh problems as difficult as those solved. There is no adequate explanation for this change from one digestive system to another; and the intermediate stages are, to so whe least, difficult to imagine.

Echinoderm Affinities. Unlikely as it seems at first sight, the best clues to chordate relationships are to be found in a study of the echinoderms—the starfish, sea urchins, and the like. Several lines of work suggest that, despite the obvious and strong contrasts, the two phyla are nevertheless related. In most vertientees meederm formation is a complex process, but in Amphicoxus we find mesoderm forming from gut pouches just as it does in echinoderms. Another item of interest is the fact that in certain of the hemichordates there is a ciliated larva (Fig. 12) of the same type as that of echinoderms—so similar, in fact, that until the life history was known, the hemichordate larvae were thought to be those of starfish!

Even biochemistry helps to establish the case. The proteins of blood serum vary greatly from form to form, and it appears in general that the more closely related two animals are, the more similar are these proteins. Tests of the sera of acorn worms and other lower chordates show their definite relationships to those of echinoderms, but not to other invertebrates. Again, muscle chemistry tends to link the two groups. In all animals with musculature, phosphorus compounds are present which speed up the energy release for muscle activity. In vertebrates a material combined with the phosphate is creatine (d. Chap. 9); in most nonvertebrate groups another compound, argenine, is present instead. But some ethnic-derms have creatine as well as argenine, is present instead. But some ethnic-derms have creatine as well as argenine, is present instead.



Fig. 12. Diagrammatic side views of the larvae of (A) an acorn worm, (B) a starfish, and (C) a sea eucumber, all much enlarged. The black lines represent ciliated bands. The digestive tract (stippled) appears through the translucent body. Views are from the left side: the larvae are bilaterally symmetric. (After Delage and Héronard.)

cates and present (as well as creatine) in some hemichordates—facts which tend further to link the two groups.

Chordate Phylogeny. What do these resemblances mean? Surely the vertebrates and their chordate relatives are not derived from echinoderms, with their specialized organs and skeletal plates, and their pronounced radial symmetry. Such a form as a starfish or a sea urchin is obviously far off any line leading to a vertebrate. But one important point may be kept in mind. Most echinoderms are free-living and capable of locomotion to some degree; but the fossil record clearly proves that the ancestral echinoderms were esselie forms and one group of living echinoderms, the crinoids or sea lilies, are fixed in habitus. Attached by a stalk to the sea bottom, they spread out above their compact bodies a series of feathery arms, ranged the length of these arms are bands of cilia which filter out from the water the food particles upon which the sea lily subsists and carry them down to the mouth.

Here lies, one may believe, the clue to the whole story. This mode of life is precisely that of the little pterobranchs which, we have seen, are unquestionably related to vertebrate ancestry despite their simple structure and the absence in them of almost every diagnostic character of vertebrates and even of chordates in general.

Despite the contrasts between primitive echinoderms and pterobranels, the two can be derived readily from an ancient common ancestor and, except for the little proboscis and a collar development which tend to tie them to the acorn worms, the pterobranels are certainly close to the pattern expected in this ancestor.

th seems clear that we must abandon preconceived ideas that the ancestral chordate was an active, bilaterally-shaped swimmer, and accept the evidence indicating that this ancestor was a sessile bottom dweller, subsisting on food particles gathered and brought to the mouth by outstretched lophophore arms. On this basis a reasonable theory of chordate evolution can be erceted (Fig. 13). Little animals of this character, collecting food by lophophore arms, are not uncommon today, notable being brachlopods or lamp shells (so called because the body and lophophore are protected by a paired shell) and the tiny bryozoans—the "moss animalcules." These forms are suspected of at least distant relationships to echinoderms and chordates, and the chordate ancestor was rather surely one of a series of such lophophore-bearers. From it, with elaboration of varied specialized a thickning of a collar region and a small proboscis, may have come the pterobranchs.

A first major development of true chordate characters was a shift in themethod of obtaining food particles, the substitution of gill-filtering for lophophores. Even in one of the pterobranchs a single pair of gill slits has developed, apparently alding in the flow of food materials into the digestive tract. With the increase and elaboration of the gill-filtering system, lophophores were abandoned. The acorn worms, still essentially sessile although not stalked, appear to represent a side branch at this stage of evolution.

Further elaboration of the gill-straining device led eventually, in one higher branch, to the typical tunicates, in which the whole animal seems to be little more than an elaborate food-filter. But as this stage was approached, there entered, it would seem, a new adaptation which was to radically alter the whole picture of higher chordate evolution.

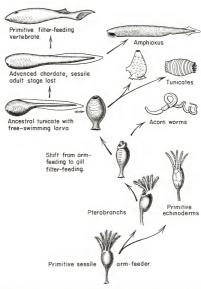


Fig. 13. A diagrammatic family tree suggesting the possible mode of evolution of vertebrates. The chinochem may have arisen from forms not too dissimits to the little pretomatic, the zown work, from pierobranch descendants which had evolved a gill-feeding system but were little more advanced in other regards. Functioner prepares at sage in which, in the adult, the gill apparatus has become highly evolved, but the important point is the development in some tunicates of a free-swimming larva with advanced features of note-ford and nerve cord and free-swimming habits. In further progress to Amphicous and the vertebrates the old sessile adult stage has been abundoued, and it is the larval type that has initiated the advance. (From Romer, The Vertebrate Story, University of Chicago Press)

The embryo or larva of a sessile organism must find a proper place on the sea bottom on which to settle down for adult life. How to reach and select it? Some acorn worms, we have noted, have a ciliated larva; but such a larva's powers of locomotion are limited. Much better is the tadpole-like larva which may have developed hefore the tunicate level was reached. Here a muscular tail is present; a notochord stiffens the structure; a nerve cord and nerves are evolved to supervise locomotion; sense organs are developed which guide the movements of this new swimming structure toward a proper place for fixation and adult existence.

Once this new larval structure was evolved, a radical change of direction in chordate evolution opened out. A new active type of life became possible. Conservative forms remain as funicates. But for others, paedogenesis appears to have entered the picture. The animal ceased to "settle down." The larval locomotor structures were retained throughout life, even though filter-feeding long continued to be the means of sustemance; the pharyageal filtering apparatus could be transported from place to place as favorable opportunities presented themselves. Amphioxus, although a bit off the direct ascending line, represented a more advanced stage, in which filter-feeding persists but the ancestral fixed adult condition has been abandoned. But for the most part, chordates did not stop at this level. A major burst of evolutionary activity resulted from the development of these new locomotor potentialities and led on to the major story of vertebrate evolution.

"Visceral" and "Somatic." In later chapters we will frequently encounter the terms "visceral" and "somatic"—visceral and somatic macles, visceral and somatic mescles, visceral and somatic merves. The "visceral"
structures have mainly to do with the gut and its appendages (particularly the
pharynx); the "somatic" structures are those of the "outer" tube of the body. One
might assume that the two terms had a mere topographic meaning and nothing
more. But it is highly probable that there is a long phylogenetic history behind
visceral-somatic distinctions (Fig. 14).



Fig. 1.8. Diagrams to show the contrast between "visceral" and "somatic" components of the chordate body. A. A theoretical type of chordate essentially similar to the tunicate larva, but with the somatic component retained in the adult, below, a true vertebrate. The area of the visceral component is outlined in black. In A the somatic animal lies posterior to the visceral animal (representing the ancestral chordate), except that sense organs and anterior part of the enercy cord estend forward doesally, In B, the visceral and somatic components overlap to a considerable degree and integration of the two is advancing.

Such a lower chordate as a solitary tunicate consists of little else than a party and appended gut tube, plus such necessary additions as the gonads and a very simple nervous system. Except that it is, of course, sheathed externally by skin or tunic, the whole animal represents essentially the visceral component of the vertebrate. The somatic component is the new, added series of locomotor devices—swimming muscles, notochord and, for their direction, a more highly evolved nervous system and sense organs. At first these somatic structures were for the most part appended posteriorly to the visceral animal. As vertebrate evolution progressed, the two became more broadly overlapping and coordinated with one another. But even today, as seen in development and in adult structure, the original distinctions tend to persist. In many ways one can regard a vertebrate as two distinct animales, visceral and somatic. The two are welded into a single structure, but some traces of the distinctions between them still persist; the "weld" is an imperfect one.

# 3

# WHO'S WHO AMONG THE VERTEBRATES

The study of organs and organ systems and their varied forms and functions—the main concern of the present work—gives us but a one-sided account of the vertebrates. What one should know is not merely the discrete parts, but the total animal; its life and its place in nature. Our present study no more gives us a rounded picture of the vertebrates than the dissection of a cadaver and a course in physiology would give us a complete knowledge of mankind. It is to be hoped that the student will read some work on the "natural history" of vertebrates and thus gain an idea of the living animals whose bodies are verbally dissected in this volume. We shall here give merely a brief survey of the membership of the vertebrate groups in order to place the forms discussed within a phylogenetic framework.

## THE GEOLOGIC RECORD

The fossil record and the extinct animals included in it require attention in this regard. In comparative anatomy one compares the organs of existing members of different groups as if one had descended from the other; as if mammals had descended from the existing reptiles, and these from existing amphibians and fishes. Obviously, however, this is not the case. A turtle is a reptile, but it is not a mammal ancestor; it has had just as much time to diverge from the common primitive reptilian stock as has the mammal. A frog is an amphibian; but it is definitely not the sort of amphibian from which more progressive land vertebrates were derived. Only through paleontology, the study of fossils, can we hope to discover the true nature of the common ancestors from which the varied living vertebrates arose.

In discussing fossils, some notion of the geologic time scale is necessary (cf. Table 1). The earth's history of several billion years is divided by geologists into

Table 1. Geologic Periods Subsequent to the Time When Fossils First Became Abundant (The Carboniferous is generally subdivided into two periods, Mississippian [earlier] and Pennsylvanian [later]. The time estimates are based on the rate of disintegration of radioactive materials found in a number of deposits.)

ERA (AND DURATION)	PERIOD	ESTIMATED TIME SINCE BEGINNING OF EACH PERIOD (IN MILLIONS OF YEARS)	EPOCH	LIFE
Cenozoic (age of mammals; about 70 mil- lion years)	Quater- nary	1	Recent	Modern species and subspecies; dominance of man.
			Pleistocene	Modern species of mammals or their fore- runners; decimation of large mammals; widespread glaciation.
	Tertiary	70	Pliocene	Appearance of many modern genera of mam- mals.
			Miocene	Rise of modern subfamilies of mammals; spread of grassy plains; evolution of graz- ing mammals.
			Oligocene	Rise of modern families of mammals.
			Eocene	Rise of modern orders and suborders of mammals.
			Paleocene	Dominance of archaic mammals.
Mesozoic (age of reptiles; lasted about 155 million years)	Creta- ceous	135		Dominance of angiosperm plants commences; extinction of large reptiles and ammonites by end of period.
	Jurassic	180		Reptiles dominant on land, sea, and in air; first birds; archaic mammals.
	Triassic	225		First dinosaurs, turtles, ichthyosaurs, plesio- saurs; cycads and conifers dominant.
Paleozoic (lasted about 375 million years)	Permian	270		Radiation of reptiles, which displace amphib- ians as dominant group; widespread glaci- ation.
	Carbon- iferous	350		Fern and seed fern coal forests; sharks and crinoids abundant; radiation of amphib- ians; first reptiles.
	Devo- nian	400		Age of fishes (mostly fresh water); first trees, forests and amphibians.
	Silurian	440		Invasion of the land by plants and arthro- pods; archaic fishes.
	Ordo- vician	500		Appearance of vertebrates (ostracoderms); brachiopods and cephalopods dominant.
	Cam- brian	600		Appearance of all major invertebrate phyla and many classes; dominance of trilobites and brachiopods; diversified algae.

a few major time units termed eras; these are subdivided into a number of periods. For the earlier eras there is little adequate knowledge of life of any sort; the fossil record is almost entirely confined to the last three eras, spanning somewhat over half a billion years of earth history.

The first of these three, the Paleozoic Era or Age of Ancient Life, covered about 370 million years, and is divided into half a dozen periods. The fossil record remaining from the seas of the oldest period (Cambrian) contains abundant representatives of almost every major animal group, except the vertebrates. The first faint traces of backboned animals have been found in the rocks of the following Ordovician period, and a modest number of archaic fishes have been found in the Silurian period that followed. The paucity of early vertebrate fossils may be the result of the group's having evolved in fresh waters; the sediments of the older Paleozoic periods are mainly marine. In the Devonian period fishes were abundant in fresh-water deposits-so abundant that this period is sometimes termed the Age of Fishes-and many had invaded the seas as well. The continental sediments of the Devonian indicate to the geologist that much of the land was subject to marked seasonal droughts, as are certain tropical regions today; times of abundant rainfall alternated with seasons when streams ran dry and pools were stagnant. These conditions appear to have had a major influence on the history of fishes and in the development of terrestrial life.

At the very end of the Devonian appeared the first land vertebrates, the amphibians, and primitive members of that group are common in the swamp deposits that characterize the Carboniferous period, the age during which the earth's major coal seams were formed. Before the end of that period the first reptiles had evolved, and early reptile orders were common land animals in the Permian period, with which the Paleozoic Era closed.

The Mesozaic Ea, the "Middle Age" of the story of life, is frequently termed the Age of Reptiles, for members of that class dominated the land life of that era, and many types of reptiles now extinct flourished in the seas and in the air as well. The highest of vertebrate groups, further, had their beginnings in the Mesozoic; the oldest mammals appeared at about the boundary between Triassic and Jurassic periods and the oldest known birds appeared toward the end of the Jurassic, but both groups remained inconspicuous till the end of the era.

The Cenacia Erā is the Age of Modern Life or Age of Mammals. At the end of the Mesozoic the reptile hordes became greatly reduced, leaving that class of vertebrates in its modern impoverished phase. Modern bird types appeared early in the Cenaciac, and, most conspicuously, the mammals rapidly evolved into the varied progressive groups which dominate the land today.

# VERTEBRATE CLASSIFICATION

The backboned animals constitute the subphylum Vertebrata of the phylum Chordata. The next step in classification is a division of the varied vertebrates into a series of classes. The distinguishing features of certain of these classes are obvious to anyone who has the slightest familiarity with nature. The class Mammalia includes the mammals, the familiar warm-blooded, hair-clothed animals among which man himself is to be included; the birds, class Ares, are readily distinguished by the presence of feathers and wings and by their possesion, qually with mammals, of a high, controlled body temperature. The class Reptilia,

lacking the progressive features of the birds and mammals, represents a lower level of land life, with lizards, snakes, turtles, and crocodiles as living representatives. A fourth group is that of the class Amphibia, including frogs, toads, and salamanders—four-legged animals, but reminiscent of fishes in many respects.

One commonly lumps the remaining lower vertebrates as "fish," and these forms (or most of them) are sometimes included in a single vertebrate class—the attitude being that, after all, they seem to be built on a common plan, as water dwellers with gills and locomotion performed by fins rather than limbs. But this is a rather personal, human viewpoint. An intellectual and indignant codifish could point out that this is no more sensible than putting all land animals in a single class, since, from his point of view, frogs and men, as four-limbed lung-breathers, are much alike. Actually, when we look at the situation objectively, a codish and a lamprey, at two extremes of the fishy world, are as different structurally as amphibian and mammal. The fishes are perhaps best arranged in four classes of lower vertebrases class Agnatha for javless vertebrates, such as the living lampreys and fossil relatives; class Placoderni for primitive jawed fishes of the Palcozoic, now extinct; class Choatchthytes, cartificiance sheeks, sharks, and their claives; class Osteichthyes, the higher bony fishes which today constitute most of the piscine world.

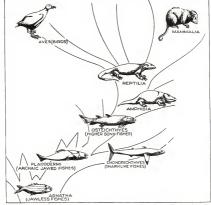


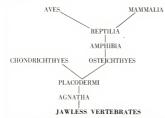
Fig. 15. A simplified family tree of the classes of vertebrates. (From Romer, The Vertebrate Story, University of Chicago Press.)

If we wish to group these eight classes, we may for convenience consider the four higher land groups as constituting a superclass Tetrapoda, or four-footed animals, the fishes as making up a superclass Pises:

Superclass Pisces. Class Agnatha
Class Placodermi
Class Chondrichthyes
Class Osteichthyes
Superclass Tetrapoda. Class Amphibia
Class Areptilia
Class Aves
Class Aves
Class Aves
Class Aves
Class Aves

This is but one of several alternative methods of grouping the vertebrate classes. Some, placing emphasis on the development of jaws, would contrast with the Agnatha all the remaining vertebrates as Gnathostomata, "jaw-mouthed" forms. Still another grouping is to consider the three highest classes as forming a group termed Amaiota, the remaining five constituting the Anamaiota. This is based upon the fact that the lower types generally have a rather simple mode of reproduction, with eggs laid in the water and young developing there, whereas repitles evolved a shelled egg, laid on land, within which a complex sort of development (described in a later chapter) takes place. Some repitles and nearly amammals bear their young alive, but have retained the same general pattern of embryonic development, and the name Amniota is derived from the amnion, one of the membranes surrounding the growing embryo in mammals and birds as well as repitles.

A synoptic classification of vertebrates is given at the end of the book. In its simplest form the phylogeny of the vertebrate classes (Fig. 15) may be diagrammed thus:



Living lampreys and hagfishes, together termed cyclostomes (Figs. 16, 17), are representatives of a lowly group, the class Agnatha—javeless verterbrates. Best known is the marine lamprey (Petromyzon). This fish is cel-like in appearance, but much more primitive in its structure than true cels (which are highly developed hony fishes). The lamprey is soft-bodied and scaleless and, though having a

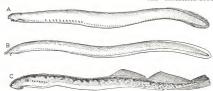


Fig. 16. Three types of cyclostomes. A, The slime hag, Bdellostoma; B, the hagúsh, Myxine; C, the lamprey, Petromyzon. (From Dean.)

feeble skeleton of cartilage, lacks bones entirely. There are no traces of paired fins, and, most especially, jaws are totally lacking. The adult lamprey is predaceous, nevertheless; the rounded mouth cup forms an adhesive disc by which it attaches to the higher types of fishes upon which it preys, and a rasping tongue-like structure within the mouth is a fairly effective substitute for the absent jaws. There is but a single mostril, opening high on top of the head, and having a hypophysical pouch (cf. p. 344) combined with it. The gill passages are not slite as in typical fishes, but spherical pouches, connected by narrower tubes with gut and body surface. In various less obvious structural characters, noted in later chapters, the lampreys likewise show a series of features in which they differ from typical fishes—features which appear to be in part primitive, in part abherrant.

The excessively slimy hagfishes are, like Petromyzon, marine in habit, but differ in a number of ways. The rasping tongue is present, but the mouth is surrounded by short tentacles instead of a sucker. The hags are scavengers rather than active predators, burrowing into the flesh of dead or moribund fishes. The nostril is at the tip of the snout rather than atop the head, and the gill pouches in some hagfishes do not open directly to the surface but join to a common external opening on either side.

The hagish eggs are laid in the sea and the young develop directly there; the marine lamprey, in contrast, has a distinct freshwater larval stage Every spring, lampreys run up the streams to spawn, and the developing young spend several years of their lives as little larvae (ammoocetes) which lie nearly buried in the mud of brooks and streams. These larvae are not at all predaceous; there is no tongue rasp, no mouth sucker. Instead, they are filter-feeders, which strain food particles much as does Amphioxus. A stream of water is brought into the mouth by ciliary action, passes through a pharynx which even has a structure—comparable to the Amphioxus endostyle, and thence flows out the gill slits. At the end of the larval period there is a sudden marked change in structure—a metamorphosis—and the young lamprey, with adult features fully developed, descends to the sea. It is possible, however, for lampreys as adults to remain in fresh waters—the sea lamprey has successfully invaded the American Great Lakes—and certain small fresh-waters species of lampreys never take up a predaceous life, but reproduce and die shortly after metamorphosis in their native streams.

It is generally agreed that the absence of jaws, and, probably, of fins, is a primitive feature of cyclostomes. Other characters, however, are more dubiously



Fig. 17. Longitudinal section of a dime log, Bdellostom. A. Amus AO, extral sorts; AP, abdomin porce: AP, atturn of heart; B, brings; BR, gill power, C. duet from susqi git to throat; D, horry, toofblic structures; DA, doesal sorts; DR, dorsal far rays; I, intestine; BO, internal gill openings; IV, softeral sact, N, sontral sact, N, sontral

primitive. There is considerable reason to regard the absence of a bony skeleton as a degenerate feature; the predaceous or scavenging habits can hardly have been present in ancestral vertebrates (mutual cannibialism is not, to say the least, advantageous), and the tongue rasp is a cyclostome specialty. Cyclostomes represent a primitive level of vertebrate development; they are not, however, in themselves ancestral vertebrates.

When we look into the fossil record, we find that the oldest and most primitive of fossil vertebrates, found in Ordovician and Silurian deposits, mainly fresh water, and surviving into the Devonian, were small fishlike creatures known as ostracoderms (Figs. 18, 19). Superficially there is little resemblance to the cyclostomes, but study shows that ostracoderms were jawless ancient representatives of the class Agnaths. In a majority of ostracoderms there was, as in cyclostomes, but a single nostril, and that high atop the head. Many ostracoderms (like cyclostomes) lacked paired appendages, although in some there were paired spines or peculiar flaps projecting from the body behind the head.

The ostracoderms were, in the absence of jaws or other biting or rasping structures, nonpredaceous. We find that in most of them there was a greatly expanded "head" region, most of which was occupied by large gill chambers (Fig. 232, p. 248). It seems obvious that these oldest vertebrates, like their chordate ancestors and like the larval lampreys of today, made their living by straining food materials through their gill system. Many of them, although capable of locomotion with a fishy tail, were much flattened and must have been relatively sluggish animals.

A major contrast with the modern cyclostomes lies in the skeleton. All ostracoderms were covered by a good bony armor, and in certain of them there was developed an internal bony skeleton as well. It was formerly assumed that the primitive vertebrates were (like the living cyclostomes and sharks) boneless forms, with a skeleton of cartilage only. This may have been true of the still older ancestral chordates and immature ostracoderms. But the prevalence of hone in the oldest known fossil vertebrates, and evidence of reduction instead of increase in ossification in the later history of many fish groups, suggest that ancestral vertebrates were armored as adults, and that absence of bone in the lower living vertebrates is a degenerate rather than a primitive characteristic. As to the reasons 38

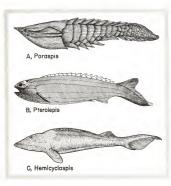


Fig. 18. Fossil ostracoderms. A. Poraspis, representative of a group (Heterostraci) in which the nostrils were presumably paired and ventral in position. The gills opened by a common slit behind the main armor plates on either side. B. Pterolepis, member of a group (Anaspida) of relatively active swimmers. The tail is tipped downward, the reverse of the shark condition. The gill openings are rounded circles on the flank; small spines are present at the point where paired pectoral and pelvic fins develop in higher fishes. The nostril opening lay dorsally between the eves. C. Hemicyclaspis, a member of the Cephalaspis group (order Osteostraci). The head and gill region are enclosed above in a solid, bony shield. The nostril opening is, again, placed dorsally between the orbits. The gills opened ventrally beneath the broad "head" (cf. Figs. 19, B; 232, p. 248). Flipper-like structures are seen in the position of pectoral paired fins. (A and C after Heintz: B after Kiaer.)

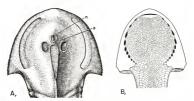


Fig. 19. A, Dorsal and B, ventral views of the head region of a fossil outracederm of the Cephilaspis type (cf. Fig. 15, C). Dorsally are seen openings for the paired eyes, median eye (p), and a median slit (a) for nostril and hypophyseal asc. Ventrally, the throat was covered by a measir of small plates, covering an expanded set of gill pouches (Fig. 232). Roand openings on either side are for the gill orifices; the month is a small anterior slit. (differ Stensio.)

for this early development of bone, we are none too certain. One suggestion lies in the fact that we find in association with the oldest vertebrates, in the stream deposits in which they are found, remains of eurypterids—ancient water scorpions and less familiar crustaceans termed ceratiocarids. Both of these arithropod types were voracious and, on the average, considerably larger than the little ostrocoderms amidst which they lived. It may be that in their earliest phases the vertebrates were the underdogs in the world of fresh-water life, bony armor may have been a defense against these invertebrate enemies. Later, as vertebrates became larger, speedier, and themselves predaceous, the eurypterids vanished from the fossil record and the ceratiocarids shrank to insignificance.

#### PLACODERMS

The ostracoderms were at the peak of their development during the Silurian.
At the end of that period there appeared somewhat more advanced fish types
which were exceedingly prominent in the following Devonian period, but became
extinct before the close of the Paleozoic. These were mostly grotesque forms,
quite unlike any fishes living today. It is far from certain that they form a truly
natural group, but they are currently considered to form a special class of vertebrates, the Placodermi, the name referring to the fact that most were, like ostracoderms, covered to a variable degree by armor plating.

All had jaws. This represents a major advance over the ostracoderms, one which opened up new avenues of life to fishes and enabled them to become more active and wider-ranging animals. The term gnathsotone—"jaw-mouthed"—is often applied to placoderms and all higher vertebrates in contrast with the Agnatha. The jaws of placoderms, however, are frequently of peculiar types and are seemingly primitive or aberrant in build—nature was still "experimenting" with these new structures. Paired fins, too, were developing, in connection with the new freedom which fishes were acquiring, but these structures also were variable and often oddly designed (from a modern point of view). The early placoderms were essentially fresh-water dwellers, like the ostracoderms before them; but during the Devoindan, many of them had invaded the seas.

Of placoderms, the most "normal" in appearance were the acanthodians (Fig. 20, A), usually termed "spiny sharks." The general body proportions were sharklike, but the acanthodians were most unsharklike in other respects-particularly the fact that they were fully clad in well-developed bony scales comparable to those found in some of the higher bony fishes. The fins mainly consisted of spines-sometimes of large size-with, apparently, but a small web of skin behind them. More common in much of the Devonian were the arthrodires-jointednecked fishes (Fig. 20, B). In these the head and gill region was covered by a great bony shield, and a ring of armor sheathed much of the body, the two sets of armor connected by a pair of movable joints (hence the name). Peculiar bony plates served the function of jaws and teeth. The posterior part of the body was quite naked in typical arthrodires. In some forms there have been found true paired fins, but in the most primitive arthrodires all we find is a pair of enormous, hollow, fixed spines projecting outward from the shoulder region-some sort of holdfast or balancing structures. Related to the arthrodires were the antiarchs of the Devonian (Fig. 20, C)-grotesque little animals which had two sets of armor like the arthrodires, but small heads, tiny nibbling jaw plates and, for limbs, a

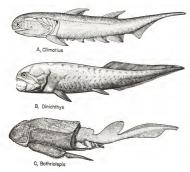


Fig. 20. Fossil Devonian placoderns. A. An acanplacoderns. A. An acanplacoderns. A. An acanplacoderns. An acanplacoderns. B. Between pectoral and pelvic pairs.
B. Giant arthrodire with 
"bead" and thoracic armor 
plating and a naked body. C. An antiarch with peculiar bony "limppers" in 
the place of pectoral fast.
(A. data from Watson: B 
after Heintr: C after Patten.)

pair of jointed "flippers" projecting from the body like bony wings. Still other (but poorly known) placoderms had reduced armor and more normal fin development and rather suggest a transition from armored ancestors to shark types.

Most of the placoderms were obviously far off the main lines of vertebrate evolution, and few, if any, of the known types may possibly be regarded as actual ancestors of latter vertebrates. As a group, however, they appear to represent nature's first essay in the development of jawed vertebrates. Most of these "experimental models" were not, in the long run, successful; others—poorfy known or still unknown—paser rise to the two classes of more advanced faises.

#### SHARKLIKE FISHES

The modern sharks are the typical representatives of a major surviving group of jaw-bearing marine fishes—the Chondrichthyes. This name, "cartilaginous fishes," refers to the fact that bone is unknown in any member of the group. It seems probable that the absence of bone in sharks is due to a process of reduction; the totolklike dentities present in the shark skin and the spines sometimes present on the fins appear to be the last remnants of the armor which once sheathed their placoderm forebears.

The sharks are almost purely predaceous in habits and with few exceptions are purely marine. Except for skeletal degeneration, the sharks appear to be in general "proper" fishes of a fairly primitive type. Absent are the peculiarities of the cyclostomes and the curious structural "experiments" seen in grotesque arthrodiress. The nostrils are double, and placed beneath the tip of the snout; there are

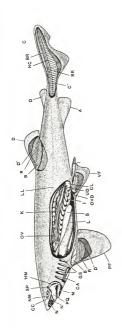


Fig. 21. Diagrammatic dissection of a formate shark, A, Anal fir; B, basal elements of fir; BR, basal and radial elements, upper and lower lobes of caudal fir; Coundal fin; C', centrum; CA, conus arteriosus; CG, cartilaginous cranium; CL, cloaca; D, dorsal fins; D', dermal rays of fin; GS, gill slits; HM, hyomandibular; I, anotine with apriat valve, R, kidnor! II, liver, III, lateral line, M, manibide, N. N', anterior and posterior openings to ausal pouch; NG, notochord; NM, "nic-titating membrane" of eye, OF, ovary; OFD, oviduct; PF, pectoral fin, PQ, upper jaw cartilage; R, radials of fin; S, stomach; SF, spiracle; UD, urtnary duct; PF, pelvic (ventral) fin. (From Dean.)

well-formed jaws, although, in the absence of bone, there is no formed skull and the upper jaws are independent of the braincase. The gills border slitlike passages, typically five in number, which open separately to the surface, and there is generally a small accessory anterior opening (the spiracle). There are well-developed paired fins, and a powerful tail fin, with the tip of the body curving into its upper lobe. A feature of sharks and their relatives which is probably not primitive is the fact that they produce large eggs containing considerable yolk. These eggs are, in many members of the group, encased in a horny shell before they are laid. To effect this, they must be fertilized before leaving the mother's body, and the male sharks have developed "claspers" projecting from the pelvic fins to aid in introduction of the sperm. Internal fertilization allows the possibility of development of the young within the body of the mother. In various sharks and rays the fertilized eggs are retained in the mother's reproductive tract, and develop there, so that the young are born alive. (Many reptiles and nearly all mammals have similarly developed this procedure.) Sharks first appear in the latter part of the Devonian, and Cladoselache (Fig. 22, A) of that period is a form

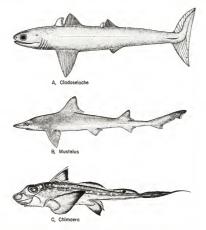


Fig. 22. Cartilaginous jawed fishes. A, Primitive Devonian shark; B, a modern shark type; C, a chimaera. (A after Dean and Harris; B after Garman; C after Dean.)



Fig. 23. A skate, Dasybatus. The pectoral fins are enormously expanded, the tail is reduced to a whiplash. The spiracle is placed just behind the eye. (After Garman.)

which may be roughly ancestral to many, if not all, of the later cartiliginous fishes. There was a variety of shark forms in the seas of the late Palezonic, and toward the end of the Mesozoic we find shark types similar to those in modern oceans (Figs. 21; 22, B). In the Mesozoic, too, there appears the first of the shares and rays (Fig. 23), forms derived from sharks; they have taken to a molluse-eating diet and a bottom-dwelling mode of life with which is correlated the flattened body shape of these unattractive fishes. In typical rays the tail and pelvic fins are much reduced, but the pectoral fins greatly expanded and, stretching forward above the gill openings, may meet in front of the head; locomotion is accomplished by undulatory movements of these broad appendages. Since in a resting position the mouth may be buried in the mud or sand of the sea bottom, the spiracle (small or even absent in sharks) is here a large opening behind the eyes through which water enters the pharvnx.

A distinct group of cartilaginous fishes is that of the chimaeras or ratchsh the Holocophali (Figs. 22, C. 24, p. 44), which are relatively rare oceanic forms. These are, like the skates, mainly mollusc-eaters; but the body is not greatly depressed, and their peculiarities include, among other features, the development of large total plates, and of upper jaws which (in contrast to those of sharks) are solidly fused to the braincase. A flap of skin covers the gill region (much as does a erries of bony plates in both placoderms and higher bony fishes). It is presumed that the chimaeras were derived from the early sharks; the fossil record, however, is imperfect.

#### BONY FISHES

The class Obseichthyes includes the vast majority of fishes. As the name implies, they are forms in which a bony skeleton has been retained, and improved upon. A characteristic pattern is to be found, with variations, in most members of the group, in the bones of the skull, jaws, gill coverings, and in a set of hony, scales covering the body. It was once believed that these fishes were descendants

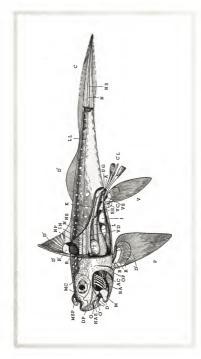


Fig. 24. Diagrammatic dissection of a male chimaeroid. A. Anus; AC, conus arteriosus; B, basal element of fin; BA, branchial arches; C, caudal fin; CL, clasper; D. dental plates; D', dermal rays of fin; D'', dorsal fins; DP, small dermal plates of lateral line canal; I, intestine with spiral valve; IN interneural cartilages of vertebral column; K, kidney; L, liver; LL, lateral line groove; M, lower jaw cartilage; MC, lateral line canals (mucous canals) of head; MSP, frontal spine peculiar to male; N, notochord; NAS, nasal pouch; NP, neural arch; NS, sheath of notochord; O. O', grooves leading to and from nasal cavity, covered by fold of skin; OP, operculum, P, pectoral fin; R, radial cartilages of fin; R', fused radials of anterior dorsal fin; SS, sperm sac; T, testis; UG, urogenital opening; V, pelvic (or ventral) fin; VC, anterior accessory clasper; VD, epididymis; VS, sperm vesicle. (From Dean.)

of sharklike forms and that bone was in them a new acquisition. It now, however, appears more probable that the bony skeleton here is simply a retention and perfection of that which was present in ostracoderms and placoderms.

The first Osteichthyes are found in rock of early Devonian age; the class is, thus, much older than the sharks. By the middle of the Devonian, bony fishes were already the dominant forms in fresh waters; and they were present in great variety and abundance in later Paleozoic periods. In the Mesozoic they invaded the seas as well, and marine waters became the headquarters of the class. Lugga appear to have been present in all primitive bony fishes, although today such structures usually have been lost or converted into a hydrostatic organ, the swim bladder. Lungs were presumably an aid to survival under conditions of seasonal drought; such conditions may have been present in the fresh waters in which the ancestral Osteichthyes lived. Later, with climatic changes and particularly with the movement of most surviving bony-fish types into the sea, the lung lost its importance.

The phylogeny of the bony fishes is complicated, but must be reviewed in order to keep in mind the position on the family tree of many interesting and anatomically important types (Fig. 25). At the very beginning of their known history the Osteichthyes had already subdivided into two major groups, termed the subclasses Sarcoptervigii and Actinopterviji.

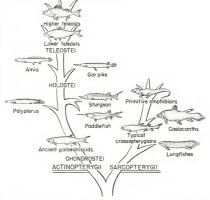


Fig. 25. A simplified family tree of the bony fishes, to show their relations to one another and to the amphibians.

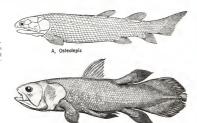


Diagrammatic dissection of a lungfish. AP, Abdominal pore; C, cloaca; CA, conus arteriosus; CC, rectal gland; CF, caudal fin; DM, dorsal mesentery; DP, tooth plates; EB, external gills; G, genital duct; GA, gill arches; GB, gallbladder; H, ceratobyal; HS, hemal spines; K, kidney; L, liver; LG, lung; LL, lateral line; M. muscle segments; M.d. lower jaw; N. notochord; NS, neural spine; ON, external and internal openings of nostril; OP, operculum; OV, ovary; P.d. pedvic girdle, PC, pericardium; PF, pectoral fin; S, scales; SW, spiral valves of intestine; U, urinary duct; VF, nelvic (ventral) fin. (From Dean.)

Surcopterygii. From the viewpoint of the descent of land animals the Sarcopterygii are the most important of the two, for they contain the order Cossopterygii, from which land vertebrates appear to have descended, and the order Dipnoi, the lungfishes, which are surviving cousins of our piscine anestests. Some of the surcopterygians have, in contrast to the other subclass, internal nostrils, as do all land vertebrates. (Because of the presence of such structures these fishes have sometimes been called the Choanichthyes.) In stronger contrast with the actinopterygians is the fact that there are fleshy-lobed paired fins (a feature to which the group name refers) and, as a technical character, scales which in early forms were of a structure quite distinct from those of the actinopterygians (the cosmoid scale, ef. p. 131).

CROSSOPTENGIANS. In the Devonian the commonest of hosp fishes were crossoptorygians (Fig. 27, A), aggressive, predaccous fishes which show important structural features of a sort to be expected in the ancestors of the amphibians. In the Carboniferous, however, they became relatively rare, and typical crossoptery-gians were extinct by the close of the Palevoire.

Meantime, however, a peculiar side branch of the crossopterygians had developed, termed the coelacanths (Fig. 27, B). These were forms with stub snouts, feeble jaws and teeth, which migrated into the Mesozoic seas. The last fossil coelacanths are found in Crotacoous rocks, and it was long taught that our crossop tergian relatives had been extinct since the days of the dinosaurs. In 1939, however, to the surprise of science, a strange fish caught off the coast of South Africa proved to be a coelacanth. This single specimen was, unfortunately, incompletely preserved; recently, however, other, better specimens have been obtained from deep waters off the Compost Islands in the Indian Ocean, and their structure is being studied intensively by French scientists. Knowledge of the structure of this his highly important, since we have here the closest lining fish relative of the tetrapods. But it must be kept in mind that the coelacanths have changed markedly in habitat during their long history. It is bence probable that many of their structures may have become specialized in correlation with changed habits rather than retaining truly ancestral conditions.



B. Latimeria

Fig. 27. Crossopterygians. A, Typical Devonian form; B, the only living coelacanth. (A after Traquair; B after Millot.)

LUNGFISHES. The Dipnoi, or lungfishes (Figs. 26, 28), are represented today by three genera, living, one each, in tropical regions of Australia, Africa, and South America. In many anatomic features and in their mode of development the lungfishes closely resemble the amphibians, and they were once thought by many to be actual amphibian ancestors. But it is now more reasonable to believe that these features were present as well in their relatives, the ancestral crossopterygians, and that the lungfishes are to be regarded as "uncles" rather than the actual progenitors of land vertebrates. The skull structure of lungfishes, living and fossil, is of a peculiar type obviously unlike that of a proper amphibian ancestor, and ossification is much reduced in the skeleton as a whole. In connection with a diet of invertebrates and plant materials, there are present in all lungfishes specialized fan shaped toothplates. It is of interest that the lungfishes have survived only in regions where we find today conditions of seasonal drought similar to those which we believe to have been present in the Devonian. The Australian form can survive in stagnant water by air breathing; the other two are able to withstand even the complete drying up of the water by digging a burrow in the mud in which they "hole up" until the wet season of the year comes round. So dependent is the African lungfish on air, that it will "drown" if kept under water.

Actinopterygii. As types ancestral to higher vertebrates, the Sarconterygii are of major interest; but as successful fishes, the Actinopterygii, or rayfinned fishes, are vastly more important. From Carboniferous times on, these have been the dominant fishes. In contrast with many sarcopterygians, internal nostrils are absent; the scales were primitively of quite another type; and except in a few primitive forms there is never a fleshy lobe to the fins. Instead, as the name implies, the paired fins are webs of skin supported by horny rays.

The actinopterygians have long been divided into three groups-here con-

sidered as superorders-which are, in ascending order: the Chondrostei, Holostei, and Teleostei. The names are not particularly appropriate from the point of view of our present knowledge of the evolution of ray-finned fishes, but may be retained for convenience.

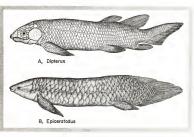
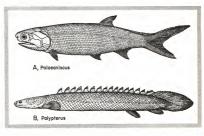


Fig. 28. Lungfishes. A, The oldest Devonian fossil type; B, Epiceratodus of Australia. The median fins have changed greatly during the history of the group. (A after Traquair: B after

Fig. 29. Primitive rayfinned fishes. A, An early Paleozoic type; B, a living representative of the ancient palaeoniscoids, with modified fin structure. (A after Traquair; B after Dean.)



CHONBOSTEL. In the Paleozoic the ray-finned fishes were represented by abundant genera of Chondrostei known as paleozoisoizoids (Fig. 20, A). These were generally fishes of small size, with rather upitted sharklike tails (the heterocreal type, cf. Fig. 121 A, p. 149) and with scales covered by a shiny material known as ganoine (cf. p. 132). (The term "ganoid" is sometimes applied to fishes of this group, but is to be avoided, for it is usually applied indiscriminately and variably to any old fish with shiny scales.) In the earliest days of bony fish history, primitive ray-finned forms were outnumbered by crossopterygians and lungfishes, but by the Carboniferous they were far more numerous than their early rivals and swarmed in the ancient lakes and streams in immense numbers and variety. In the Triassic they were still abundant, but mainly represented by advanced types transitional to the Holostei; the palaeoniscoids then rapidly declined and became extinct before the end of the Meszoic.

This primitive rax-finned group still survives in the form of three aberrant types, Two, the sturgeons and paddlefishes (both represented in North America), are rather degenerate (Fig. 30). They have lost the ganoid scale covering of their ancestors. Scales may still be present on the tail, but the paddlefish has otherwise only a naked skin, the sturgeon a partial armor of rows of plain hony plates. The internal skeleton, highly ossified in their ancestors, is nearly as degenerate as that of the sharks, for it is mainly cartilaginous, little hone remains. Degenerate, too, is their method of feeding. In both sturgeons and paddlefishes the jaws are feeble. In advance of the jaws is a sensitive rostrum which explores for food ahead of them; sturgeons and paddlefishes are bottom-dwelling scavengers or food-strainers. Only in their persistently sharklike tail fin is there much evidence of the trade-marks of the older palaeoniscoids.

The third type of chondrostean survivor is *Polypterus* (Fig. 29, B), the *bichir* of <u>Central Africa</u>, which lives in much the same environment as the lungfish of that continent. In its fins Polypterus is much modified from the ancestral type.

<sup>\*</sup>Calamoichthys is a closely related form, but with a more elongate eel-like shape, from the same region. I have made no reference to this genus in later sections, but comments on Polypterus usually apply to Calamoichthys as well.

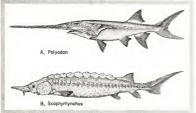


Fig. 30. Chondrosteans. A. The paddlefish or "spoon-billed cat" of the Mississippi; B, a sturgeon. (After Goode.)

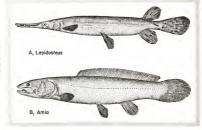
Its tail fin has become essentially symmetric; its dorsal fin is split up into a series of small sail-like structures (to which its scientific name refers), and its paired fins, unlike those of any proper actinopterygian, have a fleshy lobe. Again unique among actinopterygians is the fact that Polypterns has typical lungs, whereas other ray-finned fishes have in their place a structure termed the swim bladder (cf. p. 250), which almost never has breathing functions and is, instead, a hydrostatic organ.

Because of the presence of lungs and the fleshy paired fins, Polypterus was long considered to be a crossopterygian. But closer study shows this to be incorrect. Lungs were probably present in all primitive bony fishes, and the survival of Polypterus in peculiar drought conditions appears to be due (as with the lungshi) to their retention. Although the fins are fleshy, they differ markedly in pattern from those of crossopterygians. The <u>anatomy of the animal</u> is as a whole in agreement with that of actinopterygians rather than that of the surcepterygians, and the scales are of the true ganoid type, contrasting strongly with those of the sarcopterygians. Polypterus is surely a somewhat modified descendant of the ancient palaeoniscoids.

HIGGSTEI Succeeding the chondrosteans as dominant fishes in the middle Mesoroic were the holosteans. In them the old, long, upturned sharklike tail had become shortened, the jaws tended to have a shorter gape, and the scales in many cases, tended to lose their shing ganoid covering. Another trend, too, was apparent at this time: the ray-finned fishes were invading the seas. The major center of actinopterygian evolution from the Jurassic period onward was the ocean. The oceanic holosteans, however, are extinct (the group became rare in the Cretaceous) and the only two survivors are North American fresh-water forms. The gar pikes, Lepidosteus (Fig. 31, 4), are fast swimming fishes fairly representative of the ancestral holosteans in many ways, but specialized in their clongated jaws associated with predaceous habits. A more advanced type is Amia (Fig. 31, B), a lake and river fish of the Midwest and South, popularly termed the "dogs, hi," "mudfish" or bowfin. In these holosteans the internal selection is not at all degenerate, but in Amia the scales have lost their ganoine covering, and the tail is much like that of the teleosts.

Fig. 31. Holosteans.

A. The gar pike; B, the bowfin. Both are inhabitants of North American fresh waters and are the only survivors of a stage antecedent to the teleosts. (After Goode.)



TELEGETH. The teleosts, as the name suggests, form the end group of the cay-finned fishes, and are the fishes dominant in the world today. They appear to have originated from the holosteans in the Messzoic oceans, and before the close of the Cretaceous had replaced the older group as the most flourishing of fish types. In teleosts the originally sharklike tail has been reduced, and the tail fin has a superficially symmetric appearance. The paired fins are small; the pectorals, are usually well up the sides of the body, and may function as effective brakes the pelvic fins frequently are found well forward. The scales have lost all trace of the original shiny ganoid covering, and are generally thin, flexible, bony structures.

In the oceans where they originated the teleosts constitute (despite the presence of sharks and skates) the vast majority of all piscine inhabitants. They have invaded every possible marine habitat from the strand line to the abyssal depths. They have reinvaded fresh waters as well, where they constitute almost the entire fish population. Teleosts are unquestionably the most numerous of all vertebrates. It is estimated that there are about 20,000 different species, and the number of individuals of one species alone-the common herring-is probably on the order of a billion billion! The prosperity of the teleosts may be due in part to an efficient body organization, but is at least partially due to extraordinary fecundity. Existing bony fishes of other groups lay but a modest number of eggs; among teleosts the herring, for example, may lay 30,000 in a single season and a female cod is estimated to produce up to 9,000,000 eggs. The individual counts for little; only two eggs need to grow to maturity to keep up the numbers of the race. Because of their abundance the teleosts are a major source of human food, making available to us in highly edible form the organic materials of the oceanmaterials particularly plentiful on the relatively shallow "banks" of the continental shelves where the major fisheries are located.

The herrings and similar forms (Fig. 33, A) appear to represent a primitive group of teleosts; salmon and trout are related. The carps and calfishes are characteristic of a major fresh-water division of the teleosts. More progressive teleosts, almost all marine, are the spiny-finned forms—the perch (Figs. 32, 33, B)

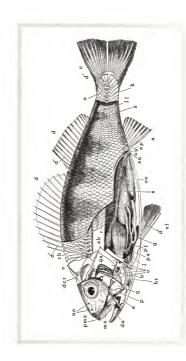


Fig. 32. Diagrammatic dissection of a teleost, the perch (Perca). a, Anal fin; ab, air bladder; an, anus; ap, abdominal pore; a', articular; b, bulbus arteriosus k, hemal spines (expanded to hypurals in tail fin); t, liver, H, lateral line; mx, maxilla; n, neural spines; no, nasal openings; o, opercular hones; or, ovary; p, nervgoid; pa, pyloric appendices, pf, pestoral fin; pmx, premaxilla; q, quadrate; r, ribs; rb, basal fin supports; s, stomach; s', scales; ug, urogenital opening; n, (comus arteriosus); br, branchiostegal rays; c, caudal fin; d, dorsal fins; d', dermal rays of fins; dn, dentary; dcr, dorsal crest of skull; g, intestine; ga, gill arches; ertebral centra; of, pelvic (ventral) fin. (From Dean.)

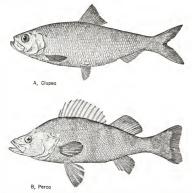


Fig. 33. Teleosts. A, Primitive type, the herring; B, an advanced, spiny teleost, the yellow perch. (After Goode.)

is typical—in which parts, at least, of the fins are supported by stout spines rather than softer rays.

Teleosts are the most versatile of vertebrates. Within both lower and higher divisions of the teleosts there has evolved a great variety of body shapes, after of which are shown in Figure 34. Equally diverse are their habits. In food they range from eaters of microscopic plant particles to predaceous forms which attack other fishes. And although they have not successfully invaded the land or air, some teleosts, such as the "climbing perch," can clamber about on land on stout fin spines, and "flying fishes," can glide above the water.

In any comparative study of vertebrate anatomy or physiology in which the eleosts are involved, their ecologic history must be kept in mind. Since land vertebrates come from fresh-water fishes, one tends to assume that structures or functions seen in fresh-water teleosts may be representative of those once present in the ancestors of the tetrapods. But we must remember that our common fishes belong to a different branch of the fish family tree from that which gave rise to land animals. It must, further, be kept in mind that modern fresh-water teleosts have not been, in all probability, continuous residents in that environment since the early days of fish history; between that time and the present there intervened a long marine phase.

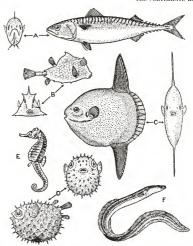


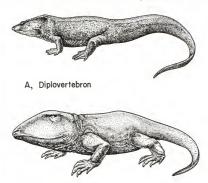
Fig. 3A. A number of teleosits, to show the variety of forms assumed by this modern fish group, A. The mackerel (Souther), a fast-swimming streamlined fish, B, The trunk fish (Ostracion), with a still body and only the fins movable. C, The marine sunfish (Mola), a very thin, deep-hodied fish adapted to quiet waters. D, The globe fish (Childemyderns), with nearly spherical contours. E, The sea horse (Hippocampus), F, A common cell (Angulla). (From Norman, A History of Falsac)

## AMPHIBIANS

Greatest, perhaps, of all ventures made by the vertebrates during their long instory was the development of tetrapods in the invasion of the land—a step which involved major changes in function and resulted in profound structural modifications. The shifts from swimming to four-footed walking, and from gill breathing to the dominance of lungs, are the most obvious of the modifications necessary in this step. But analysis shows that functional and structural changes were necessitated in almost every organ or organ system of the body.

The basic group of land vertebrates is the class Amphibia. There are three tiving orders (Fig. 36): the frogs and toads (Anura); the newts and salamanders (Lrodela); and some wormlike burrowers (Apodo). Commonest are the anurans, familiar to us it temperate regions and represented in great variety in the tropics. Their specialized nature is obvious in their jumping habits, which are responsible for many modifications in their structure, particularly in the skeletal system. The salamanders are retiring but not uncommon dwellers in moist temperate zone habitats. In their external form the salamanders resemble the ancestral amphibians which first sprang from ancestral fishes. There is a fairly elongate but stoutly built body, with powerful trunk musculature, and a well-developed tall which is an aid in swimming. The median fins of fishes are gone, but the paired fins have developed into the typical land limbs which are the trademark of the tetrapods. The Apoda for Gwmnophional will not be familiar to many readers of this work, for they include only a few genera of small, blind tropical burrowers which look not unlike earthworms.

In salamanders, and in the other modern amphibian orders as well, we find various internal features which bridge structural gaps between the crossopterygian fishes and the higher classes of land vertebrates. Amphibian structure and func-



B, Ophiacodon

Fig. 35. A. Diploverteiron, a primitive Paleozoic amphibian (labyrinthodont); B, Ophiacodon, an carly Permian reptile, representative of primitive members of that class, although showing indications of relationship to mammalian ancestry. (A after Gregory.)

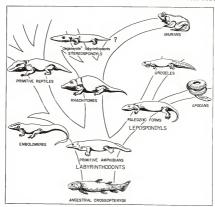


Fig. 36. A "family tree" of the Amphibia. The surviving groups are shown at the upper right. Urodeless, apedans and their fossil relatives are commonly grouped as lepospondyls, as contrasted with the labyrinthodouss, the frogs have been generally regarded a derived from lavylimbodous, but their form certain. The various groups of labyrinthodous are named from vertebral types discussed in Chapter 7.

tion are important in comparative studies. But due caution must be exercised. Frogs and salamanders and apodans are amphibians, and the amphibians are the most primitive of tetrapod classes; but we must not complete a false syllogism by concluding that these modern amphibians are really primitive tetrapods. In the modern orders the skeleton is degenerate, with considerable loss of bones from the head and, particularly in salamanders, a trend for retention of embryonic cartilages. In all, vertebral column structure is apparently quite far removed from that which was present in truly ancestral land forms, and the great shortening of the trunk and reduction of the tail in frogs shows a high degree of specialization. The limbs of newts are seemingly not too aberrant, but those of a frog are certainly highly modified; and the apodans have abolished limbs altogether. Concerning the soft anatomy, we cannot be so sure, but there are indications that here, too, many features are likewise aberrant in these modern orders. A frog is, in many ways, as far removed structurally from the oldest land vertebrates as is a man, and even a salamander must be regarded with suspicion.

For the actual ancestors of the land dwellers as a whole, we must turn to

the fossil record of the late Paleozoic when, in the Carboniferous and early Permian, there lived numerous and varied amphibians of a more primitive nature. Two major groups were then distinguishable.

One included a series of small animals, termed lepospondyls, of which a diagnostic feature is the spool-shape of the central portions of the backbone segments. It seems likely that the older lepospondyls were, despite their antiquity, a side branch, if an early one, of the basal stock of land animals. The true base is to be sought among a second early group of amphibians, the labyrinthodoms [Fig. 35, d). These animals, of variable size, were in general considerably larger than contemporary lepospondyls; some attained crocodile proportions. Their vertebral construction was a diagnostic feature and was one from which that of reptiles and higher vertebrates could have been readily derived (cf. Figs. 104, 105, pp. 138, 139). Except for the absence of median fins and the presence of short but sturdy legs developed from paired fins, many features of the early labyrinthodonts are highly comparable with those of the crossopterygians from which they came. They were the first vertebrates to walk on land.

In the late Paleozoic and earliest Mesozoic, labyrinthodonts were abundant and varied. From them at an early stage came, presumably, the lepospondyl stock from which the salamanders and Apoda have descended. The frogs have generally been considered to be an independent offshoot from the labyrinthodonts, but it is possible that they are allied to the lepospondyls; more evidence is needed.

Before the close of the <u>Paleozoic the labyrinthodonts had given origin to the reptiles</u>. With the rise of that more progressive class, the amphibians rapidly dwindled in importance. The labyrinthodonts vanished at the close of the Triassic, and the surviving amphibians play but a modest role in modern vertebrate life.

One sometimes tends to think of the development of the early land vertebrates as the result of some "urge" toward terrestrial life among their fish ancestors. This is, of course, absurd; the evolution of the earliest amphibians capable of walking on land seems to have been essentially a happy accident. The amphibians appear to have evolved from crossopterygian ancestors toward the close of the Devonian, an age during which seasonal droughts were, it seems, common over much of the earth. Lunga, already present in the ancestral fishes, are an excellent adaptation for use under stagnant water conditions. But when a stream or pool dries up completely, a typical fish is rendered immobile and dies. Some further development of the fleshy fins already present in crossopterygians would give their fortunate possessor the chance of crawling up or down the stream bed (albeit with considerable pain and effort at first) and enable him to reach some surviving water body where he could resume a normal piscine existence.

Legs, the diagnostic feature of the tetrapod, may thus have been, to begin with, only another improvement for an aquatic life. The earliest amphibian was little more than a four-legged fish. Life on land would have been the farthest thing from his thoughts (had he had any). It was probably only after a long period of time that his descendants began to explore the possibilities of land existence opened out before them through their new locomotor abilities. And even to-day those of his descendants which have remained amphibians have never capitalized fully on these potentialities.

The term amphibian implies the double mode of life exhibited by many members of this class. Some toaks spend much of their lives on good dry land, but most amphibians do not venture far from the stream hanks, and some modern forms are still essentially water dwellers like their ancestors. The typical amphibian mode of development, as exemplified by the familiar frogs and toads of northern temperate regions, is still essentially that of the ancestral fishes. The eggs are laid in the water, and develop there into water-dwelling, gill-breathing tadpoles. Only when adult size is neared do lungs replace gills, do limbs develop and mature, and does terrestrial life become possible. An amphibian is chained to the water by his mode of development and the necessity of returning to that element periodcally for reproductive purposes. Although numerous modern amphibians have adopted a variety of adaptations to avoid this complication, none has been a complete success as a fully terrestrial form. Indeed, some salamanders have, as it were, abandoned the attempt; such forms as the American "impd puppy" (Necturus) never emerge onto land at any stage, retain external gills and water-breathing, and reproduce, in paedogenetic fashion, in essentially a larval condition.

#### REPTILES

The reptiles are the descendants of the ancient amphibians which, happily, solved this reproductive problem and became the first fully terrestrial vertebrates. The "invention" of the amniote egg (with the associated developmental processes; see Chapter 5) is the major diagnostic feature which distinguishes reptiles from amphibians.

The reptilian egg is laid on land; thus there is avoided the necessity of any adaptation for water existence in either young or adult. This egg type is the familiar one preserved in the reptiles' avian descendants. The shell offers protection. A large yolk furnishes an abundant food supply so that the reptilian young (unlike the tadpole) can hatch out, at a fairly good size, as a miniature replica of the adult and thus avoid the necessity of prematurely foraging for its food. Of embryonic membranes developed within the egg shell, one sheathes externally both young and yolk. A second forms a lunglike breathing mechanism for absorption of the oxygen which penetrates the porous shell. A third (the aminon, from which the egg type gets its name) encloses the developing embryo in a liquid-filled space—a miniature replica of the ancestral pond. The development of this new egg type was so important for the later evolution of land vertebrates that, as noted earlier, the reptiles, together with the birds and mammals which descended from them are often styled collectively the amniotes.

It is probable that the oldest reptiles were still amphibious in their habits, and that the anniote egg was merely an adaptation parallel to, but better than, other adaptations seen in modern amphibians—a device which removed the eggs from the dangers of drought, and of enemies present in the ancestral waters there again, a major advance in the evolution of vertebrates may well have been a happy accident.

Modern reptiles—mainly consisting of lizards, snakes and turtles—are moderately abundant in the tropics, but unimportant in temperate zones and absent from cold climates where survival is difficult for these "cold-bloaded" creatures. The modern forms, however, are but sparse remnants of the great array of reptiles which, beginning in the late Paleozoic, radiated out into a bewildering variety of forms that long ruled the earth and caused the Mesozoic Era to be popularly known as the Age of Reptiles (Fig. 37). The basic stock from which they sprang, the long-extinct Cotylosauria or "stem reptiles" were, apart from reproductive improvements, still very archaic—clumps and ungainly, with limbs spravled out sideways from the body, and in most regards no more advanced than their amphibian forehears and cousins. But due, no doubt, to the breaking of the chains which bound them to the water, there presently developed from them the groups which became prominent in the Mesozoic.

An early side branch of the stem reptiles were the turtles—order Chelonia. In their sprawling gait they are reminiscent of their Palezozic forebears, but turtles have made a conspicuous advance in the development of a protective shell of bone, covered by horn, guarding both back and belly. Once encased in armor the chelonians turned conservative, and since the Trassic have advanced but little in most regards. The only later improvement of any note made by the order as a whole was the acquirement of the ability, lacking at first, to pull the head back into the shell. In all familiar types this is done by a straight backward pull, with the neck hent in an Securve; some odd tropical forms tuck the head in sideways against the shoulder. Like the most ancient reptiles, most modern turtles are amphibious marsh and pond dwellers. Some, however, reverted to a purely aquatic life and several marine forms have developed, with paddle-like limbs for propulsion. At the other extreme, one group, the tortoises, have become purely terrestrial.

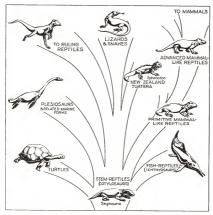


Fig. 37. A simple family tree of the reptiles (ruling reptiles not included). (From Romer, The Vertebrate Story, University of Chicago Press.)

Despite their newly-won ability to conquer the land, a number of Mesozoic reptile groups changed (like the sea turtles) to a marine existence. Two prominent Mesozoic types of this sort, now quite extinct, were the plesiosaurs and the ichthyosaurs. The plesiosaurs (order Sauropterygia) have been popularly compared to "a snake string through the body of a turtle." Plesiosaurs were not at all related to either of these two reptiles, but the description is not inapt. They possessed a long neck or long snout or both; the body was short, broad and relatively flat. Reversion to a truly fish-like means of locomotion was impossible, for turnd was inflexible and the tail short; instead, the limbs were developed into powerful oar-like structures, with which the creature "rowed" its way through the sea.

Even more unusual structurally were the *Ichthyosauria*, the "fish-reptiles." Possibly the plesiosaurs were able at least to waddle about on a beach in the fashion of a marine turtle or a seal. The ichthyosaurs, however, had become as completely adapted to a marine life as a porpoise or dolphin (with which there are many analogies), and there is fossil evidence indicating that egg-laying on land had been abandoned and that the young were born alive. The body shagus sompletely re-converted to that of a fish—the neck telescoped to give a disinform body shape, the limbs shortened into small steering devices. Locomotion was performed, fish-like, by undulations of trunk and tail; a fish-like fin was developed on the back, and the tail became a powerful swimming organ, in appearance like that of a shark. In this last regard, however, there is a notable structural difference; for whereas in a shark the end of the backbone tills into the upper lobe of the tail fin, that of the ichthyosaur turns sharply down at the back, the fin (as we know from excellent slass of fossils) expanding above.

The temple region of the skull affords diagnostic features useful in reptile classification (cf. p. 184). All the reptile stocks to be further mentioned (except the mammal ancestors) are characterized by descent from forms in which two openings, (fenestrae), bounded by arches of bone, are present in the temple and cheeks. A two-arched (i.e., diapsid) group which appeared early in the Mesozoic and has persisted to the present day, although never prominent, is the order Rhynchocephalia, now represented by the tuatara (Sphenodon). This creature, lizard-like in appearance, has survived in the relative safety and isolation of New Zealand where, once widespread, it is now preserved on a few small islands. Descended from ancient forms related to the tuatara is the much more successful order of the Squamata, the lizards and snakes. Technically they are readily distinguished by the fact that the cheek and temple region of the skull has been reduced, so as to leave but one temporal arch (lizards) or none at all (snakes) (cf. Figs. 160, 161, pp. 185, 186). The "scaled reptiles" are not only the most flourishing but the most modern of reptile orders, for even lizards amounted to little until late in the Cretaceous and the deployment of the various snake types did not take place until Cenozoic times. Lizards are widespread in the tropics in great variety. Most prominent of American lizards are the iguanas and their relatives, such as the collared lizard or "mountain boomer" of the Southwest and the little "horned toad." In the Old World the largest forms are the monitor lizards (Varanus), one of which, in the East Indies, may reach a length of a dozen feet. Relatives of the monitors in the late Cretaceous had a temporary success as a group of giant marine lizards, the mosasaurs. The (true) chameleons of the Old World tropics, with peculiar grasping feet and highly protrusible tongue, are a specialized side branch of the lizard stock. In several lines of lizards there have developed burrowing types, with limbs reduced or absent.

Derived from lizards are the snakes, which are highly modified in two major regards. As in some lizards, the limbs have been reduced and generally lost completely, and locomotion is accomplished by sinuous undulations of the body and tail, the projecting horny scales preventing backslipping; essentially, a snake swims on dry land. More distinctive is the fact that skull parts and jaw apparatus are markedly altered in the direction of flexibility and as a result allow the swallowing of the prey whole. Some snakes of primitive type are burrowers, and it is possible that snake evolution began with such forms, but even among such primitive types as the constrictors—the boas and pythons, some of great size—most now live above the surface. The great majority of snakes belong to a family of which the common harmless forms of northern temperate regions are representative. But even within this family many tropical genera have developed poison glands. These, however, are generally small and inoffensive and the fangs, situated in the back of the mouth, present little danger to man and other large animals. Three further families include the major poisonous snakes, with highly developed fangs and with powerful and varied venoms which attack the nervous system or cause destruction of tissues: (1) a group, mainly Old World, which consists of the cobras and their kin, and the coral snakes as well; (2) venomous sea snakes, found in the Indian and Pacific Oceans; (3) the vipers, with erectile fangs, including the adders and other vipers of the Old World, and the pit vipers, mainly American, with such representatives as the rattlesnakes, copperhead and water moccasin.

An exceedingly important reptile group with the same two-arched type of skull build as Sphenodon is the great subclass Archosauria, the ruling reptiles (Fig. 3B). Today they survive only in the form of the rather aberrant crocodiles and alligators; but most of the dominant land reptiles of the Mesozoic were archosaurs, and the birds are descendants of this group.

The basal stock of the archosaurs is found in the Triassic in the shape of rather small, slenderly huilt predaceous reptiles included in the order Thecodontia. Elongate hind legs, a modified hip structure and other features suggest that they were becoming adapted to a bipedal mode of life. From these modest beginnings came the dinosaurs. These are popularly considered as constituting a single group of gigantic reptiles. This concept is far from correct, for although many dinosaurs were large, some were small (one was no bigger than a rooster). There were two major dinosaur stocks, not particularly closely related to one another, although both were descended in common from thecodont ancestors.

In one group, termed the <u>Saurischia</u>, or <u>reptile-like dinasaurs</u>, the ancestral forms were bipedal carnivores. Some of the smaller and more primitive of these bipeds can scarcely be distinguished from their thecodont ancestors. Others grew to immense size: Tyrannosaurus was the most ponderous flesh eater the earth has even seen. Derived from early bipeds of this sort were the amphibious (sauropod) dinosaurs, which changed to a herbivorous mode of life, reverted from a bipedal pose to four-footed walking and grew to such giants as Brontosaurus and Diplodocus. It would appear that these great reptiles spent much of their lives in lagons where soft vegetation abounded; such was their weight (one is estimated to have reached 50 tons) that it seems improbable that their stocky limbs could have supported them effectively on land.

A second major group was that of the *Ornithischia*, or *birdlike dinosaurs*, in which the hip girdles (but not other anatomic features) were comparable to those of birds. Like their saurischian cousins, primitive members of this group

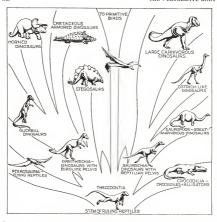


Fig. 38. A simple family tree of the ruling reptiles. (From Romer, The Vertebrate Story, University of Chicago Press.)

were bipeds; but in contrast with that other dinosaur stock, all the birdlike forms were herbivores. Best known of the bipeds of this group are the duckbills (hadrosaurs), which were abundant in the closing days of the Age of Reptiles. As in the saurischians, so in the ornithischians there was reversion to a quadrupedal pose. There were, in fact, three distinct types of quadrupeds developed in this order, all with some sort of defense against the great carnivores of the day. These types are exemplified by such popular museum exhibits as those of Stegosaurus, whose backbone is capped with defensive plates and spines; Ankylosaurus, low and flat and heavily armored on back and tail; and the horned dinosaurs, such as Triceratops, with horns—usually a trio of them—and a great frill of bone protecting the neck.

Dinosaurs flourished greatly during the Jurassic and Cretaceous, and even in closing phases of the latter period were present in considerable numbers and variety. Then, within a very short space of time, they disappeared completely. The reason for this abrupt end of the Age of Reptiles is far from fully understood. Geologic events are perhaps basically responsible. The Cretaceous period was one of mountain building during which great ranges, such as the American

Rockies, began to emerge from formerly flat country. Many of the low-lying marshy and lagoonal areas where dinosaurs browsed on lush vegetation disappeared. Climatic conditions were radically changed, and new types of plants appeared with which the herbivorous dinosaurs, with teeth generally none too ethicent, were probably unable to cope. As the herbivores consequently dwindled and disappeared, their flesh-eating cousins, who preyed upon them, would of necessity follow them to extinction.

Still another group of extinct archosaurs was that of the order Perosauria, the winged reptiles. In them the front limbs had one finger (the fourth) enormously elongated. From it there was extended, in somewhat bathick fashion, a great wing membrane. Manipulation of a wing of this sort would appear to have been an awkward matter, and it is probable that flight consisted mainly of soaring rather than active beating of the wings. Further, without any intermediate integers extending into the wing membrane to strengthen it, the dangers of a disastrous tear would seem to have been great. The hind legs of pterosaurs, quite in contrast with those of birds, were feeble structures, and it is difficult to see how these creatures could have stood upon them, much less get a running take off, as bird of any size must do. Probably they perched in bat-like fashion. But it is difficult to imagine what safe perch could be found for a pterosaur with a wing spread of up to 27 feet (as seen in one Cretaceous form). All in all, it is not difficult to understand why the pterosaurs became extinct once more efficient flying forms—the brins—had evolved.

Sole survivors today of the archosaurs are the alligators and crocodiles comprising the order <u>Crocodilia</u>. Although many of their structural features are indicative of a bipedal ancestry and descent from the theododist, the crocodilians, like many of their dinosaurian relatives, have reverted to a quadrupedal gait and have, further, become amphibious. The crocodiles are phylogenetically remote from the base of the reptilian family tree; their anatomic features are hardly to be considered characteristic of reptiles as a whole, and, as might be expected, they show numerous features found in the birds, whose ancestors were archosaur relatives of the crocodiles.

### BIRDS

Birds have been aptly termed "glorified reptiles." We customarily reat of them as a separate class, Ases, but in many regards they are little farther removed from the general reptilian stock than are some of the ruling reptiles from which they sprang. Within that group, as we have noted, was included one series of flying forms, the pterosaurs; the birds are not descended from pterosaurs, but are a second archosour flying type, in which, instead of membrane, feathers—diagnostic of the disas—form the wing surfaces of the motified pectoral limbs. In certain respects, notably bipedal adaptations, the birds are similar to their dinosaurian relatives, but almost every notable high character is an adaptation to flight. The maintenance of a high and constant body temperature and improvements in the circular tory system are associated with the need of a high metabolic rate for sustained flight; lightening of the body in various ways (particularly by the development of air seas and hollow bones) is also associated with flight, as are modifications in the brain and sense organs. The birds in the course of their evolution necessarily "discovered" long ago many of the principles of aerodynamics that man has

learned as a result of much scientific work and hard experience; they are "expert" in wing construction and in the utilization of winds and air currents in gaining distance or elevation. In general birds with an active beating type of flight tend to have small wings, those that rely mainly on gliding and soaring usually have relatively larger wing surfaces. Flying birds (in contrast to ostrich-like ground-dwellers) are seldom of any great size, in maintenance of flight, wing area must increase on the whole, proportionately to weight, and too great size of body would require a wingspread so great as to be difficult to manipulate.

Except in Mesozoic birds, teeth were lost and reliance placed on a bill for gathering food. Numerous variations are seen in bill structure, with such extremes as the parrol beak and the effective drilling organ of the woodpeckers. Presumably the food of primitive birds was of some relatively soft nature, and teeth were not necessary. Many modern birds, however, are eaters of grain. For this type of food mammals need highly developed "grinders"; birds have developed as a functional substitute a grinding apparatus in the muscular gizzard containing grit or small pebbles.

In the birds we see a class of vertebrates which in many regards is to be considered so on as high a level of organization as the manmals, but which (even disregarding differences in aerial vs. terrestrial locomotion) are organized in quite another fashion. Birds can, to be sure, be trained, but on the whole seem relatively much less capable of learning by experience than manmals. On the other hand they exhibit innate behavior patterns of a complexity unknown in mammals. Many of these, connected (for example) with social behavior, courtship, nestbuilding, and rearing of the young, are familiar to any bird-lover. Avian "knowledge" of geography is most remarkable. The homing ability of birds is great, and the ability, for example, of young golden plovers to migrate successfully from the Arctic tundras to the Chaco region of South America—unaccompanied by older birds, over a complicated course of many thousands of miles—is an accomplishment apparently verging on the supernatural.

A happy accident of preservation has given us knowledge of three skeletons of an ancestral bird, Archaeopteryx, from deposits of late Jurassic age (Fig. 39).



Fig. 39. A restoration of the primitive bird Archaeopterys, with teeth, claws in the "hand," a long bony tail and other reptilian characters. (After Heilmann.)

In this bird teeth were still present, the wing had clawed fingers, and there persisted a long reptilian type of tail; Archaeopteryx so nearly split the differences in skeletal structure between ruling reptiles and modern birds that its systematic position would be a matter of doubt were not imprints of feathers preserved with the skeletons.

Birds, mainly owing to the delicacy of their skeletons, are relatively rare in the fossil record. However, there is evidence that before the close of the Cretaceous there had evolved forms quite modern in almost every structure.

Although taxonomists divide the birds into a considerable series of orders, the structural differences between these groups are for the most part small. There is, however, one partial exception to this; for there has been thought to be a distinction between two modern groups, representing primitive and advanced stages in bird evolution. Technically, the two have been defined by details of palatial agiant structure (with which we need not here concern ourselves) which gave rise to the terms "palaeoganthous" and "neoganthous" to distinguish them. Most birds with which the reader is ordinarily familiar—indeed, the majority of all living birds—are members of the latter, higher group. To the lower assemblage (Fig. 40, A-C, E-F) belong the ostrich and other forms generally termed ratites such as the cassowary and emu of Australia, the rhea of the South American pampas, the extinct moas and the little kiwi of New Zealand, and the giant extinct birds of Madagasaca.

Most of the palaeognathous birds have tiny wings and are flightless, a fact that has given rise to the claim that they represent a primitive stage in bird evolution in which flight had not been attained. But anatomic study strongly indicates that this is not the case and that the raties are probably degenerate descendants of once flying types. (They owe their name to the reduced condition of the breast-bone, to which wing muscles attach). Most of them are found on islands where there are few terrestrial enemies, or on continents (Australia, South America)

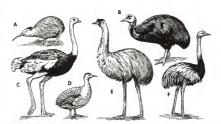


Fig. 40. Palacoguathous birds, including the ratites. A. The kiwi, Apteryx, of New Zealand. B, The emu of Australia. C, The ostrich. D, The tinamou of South America. E, The cassowary of Australia. F, The rhea of South America.



Fig. 41. Thumb-nail sketches of representative members of the major orders of birds above the ratite level. The ordinal name and the popular name of the bird representing it are given in each case.

where, the fossil record tells us, the same was true at the time that the native ratites evolved. If ground-dwelling enemies are absent, much of the "point" of fiving has been lost. The tinamous of South America (Fig. 40, D) are birds which have the power of flight (although they are awkward flyers) and yet have the "oldfashioned" type of palate; they may represent an ancestral group from which the ratites have developed.

Apart from the ratites, most birds, as has been said above, are rather uniform in basic anatomic features, with differences between orders no greater than those which distinguish the smaller groups, termed families, among mammals, To the student of habits, songs, and plumage, the birds have much to offer; they offer little, however, to those interested in anatomic structure and function. Hence the remaining bird groups may be dismissed briefly. In Figure 41 are thumb-nail sketches of representatives of the major groups of birds other than the ratites, pictured in the sequence in which the orders are listed by many ornithologists. A majority of all birds are members of the final order, the Passeriformes or perching birds, including the song birds. These highly evolved bird types are all relatively small; the crows and ravens are giants of the order. Several orders of water birds and oceanic types are customarily placed at the beginning of the series, although there is little evidence that they are actually primitive. Of special interest here are the penguins, southern hemisphere forms which are flightless but nevertheless have powerful wings which have been transformed into swimming flippers. Here, as in the case of the ratites, it has been argued that absence of flight is primitive. It is, however, more probable that they have descended from oceanic birds of the preceding order (Procellariiformes), to which belong not only the albatross and its close kin, but diving birds, which likewise use the wings in swimming. \*

### MAMMALS

Mammal-like Reptiles. The mammals are descended from reptiles; but the fossil record shows that the reptilian line leading to them diverged almost at the base of the family tree of that class. Their relationship to the existing reptilian orders is exceedingly remote.

Oldest of the reptiles antecedent to mammals were the pelyosours (Fig. 3S. p. 5S), a group which flourished in the early Permian. They were in most regards exceedingly primitive reptiles, but certain characters in skull structure (such as the presence of but a single opening in the temple region of the skull) indicate that they represent a first stage in the evolution toward mammalian status. Succeeding them in late Permian and early Triassic days were the therapsids, progressive mammal-like forms which were the commonest animals of their day (Fig. 42). The characteristic therapsids were flesh-eaters, active four-footed run-ers in which, as in their mammalian descendants, elbow and knee had been swung in toward the body, making for better support and greater speed—this in contrast with the sprawled limb pose of primitive land animals. In the advanced Triassic members of the group many features of skull, jaw, dentition, and limbs approach closely the mammalian pattern.

<sup>\*</sup> For those of literary tastes, it may be mentioned that the penguins of which Anatole France wrote are the auks of English-speaking peoples.



Fig. 42. A mammal-like reptile (Lycaenops) from the late Permian of South Africa. (After Colbert.)

The evolution of mammal-like reptiles was a major feature of early reptilian evolution. But in the Triassic period other reptile groups became prominent—notably the dinessurs. It appears that therapsids, for the most part, could not compete successfully with them, and rapidly dwindled and disappeared from the scene. There survived, however, small therapsids from which evolved the oldest mammals, sparse remains of which are found in later Mesozoic deposits. Living as they did for tens of millions of years as contemporaries of the dinosur dynasties, our small Mesozoic mammal ancestors were seemingly insignificant in the life of their times.

Intelligent activity may be reasonably regarded as the keynote of mammal-ian progress. With activity may be correlated not only the efficient locomotor apparatus characteristic of mammals, but also (as in birds) circulatory improvements and high body temperature (with which the development of hair is related). In enterprise and ingenuity even the stupidest of mammals is an intellectual giant compared with any reptile. The habit of bearing the young alive—characteristic of all except the most primitive forms—and the development of the nursing habit, with concomitant care and training of the young, are mammalian innovations which have resulted in giving a long period for the development and elaboration of delicate nervous and other mechanisms before the young are sent out into the world.

Monotremes. The monotremes, or Prototheria, include only the duckbill and spiny anteaters of the Australian region. So different are they from other mammals that it is believed that they must have diverged from the ancestors of other members of the class at the very beginning of mammalian history-indeed, quite possibly they sprang independently from the advanced therapsids. These curious animals possess many diagnostic mammalian characters, but retain primitive features in that, alone of mammals, they still lay shelled eggs like their reptilian ancestors. The duckbill is a semiaquatic, web-footed, fur-covered frequenter of streams in which it finds a food supply of snails and mussels. The anteater, protected from enemies by a coat of spiny hair, subsists on termites; its powerful clawed feet give it phenomenal digging ability. Both types make nests in burrows where the young are nursed after hatching. These two types are so specialized in many ways that they cannot be regarded as in themselves ancestral types. Their survival in Australia may be due to the relative isolation of that area. Unfortunately we know almost nothing of their history. Much of our knowledge of the relationships of extinct mammals is based on diagnostic characters of molar tooth pattern (discussed in a later chapter); the monotremes are, unfortunately, toothless (as adults), having instead horny bills—flat and duck-like in the one type, slender in the other.

Marsupials. Rare finds from the later Cretaceous tell us that there had by then evolved two more progressive mammal groups-the marsupials and the oldest placental mammals. The marsupials, or pouched mammals-technically termed the Metatheria-owe their popular name to the fact that although the young are born alive, they are born at a tiny and immature stage; typically, the female marsupial carries on her belly a pouch in which the newborn young are kept and nourished for a further period after birth. The common opossum is characteristic of the group and is a primitive mammal in many regards. In most regions of the world the marsupials have not been able to compete successfully with more progressive mammals, and even the hardy opossum failed to survive except in the Americas. South America proved a haven for many marsupials during Tertiary times, when that continent was long isolated; a variety of marsupials developed there, almost all of which became extinct when the isthmian link was reestablished and a host of more advanced mammals invaded that continent. Australia is the one region where marsupials have flourished greatly. The geologic evidence suggests that this latter continent became separated from the rest of the world at the close of the Cretaceous and has since remained isolated. No placental mammals, it appears, had reached Australia at the time of separation, and few have been able to reach it since. There the marsupials had no opposition, and expanded and diversified to fill almost every type of adaptive niche which placental mammals have occupied in other regions. Fairly directly from the ancient

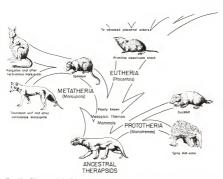


Fig. 43. Diagrammatic family tree, to show the evolution and relationship of the major groups of mammals.

opossum-like ancestors came such pouched carnivorous forms as the native "odd," and pouched parallels to anteaters and even moles of other continents. A second branch of the Australian marsupials acquired chisel-like front teeth and developed types comparable to the rodents among placentals. There are varied native squirrel-like types, even a marsupial flying "squirrel." The wombat is analogous to the woodchucks or marmots other regions; the native "bear," the koala, is a leaf-feedre belonging to this group. The marsupials have failed to parallel the placentals in one respect—there has been on development of hoofed forms comparable in structure to horses, cattle and antelopes. But the kangaroos—which, like the typical ungulate placentals, are speedy ergs-esting plains-delters—fill much the same blose in nature.

Placental Mammals. The major progressive group of mammals includes the host of living forms properly termed the Eutheria, the "true mammals," but usually called placentals. The latter name is due to the fact that, in contrast with most marsupials, there is an efficient nutritive connection, the placenta, between mother and embroy; as a result the young can develop to a much more advanced stage before birth. On the extinction of the dinosaurs, these highly developed ammmals were already in existence; they rapidly expanded into a host of types, many of which have continued down to modern times. In some other groups of vertebrates the family "tree" is actually tree-like, with a main trunk or at least major branching limbs. That of the placental mammals, however, is comparable to a great bush: the various orders are difficult to assemble into groups and appear, for the most part, to have branched out independently of one another early times. We may briefly note some of the main components of the placental assemblage (Fig. 44).

The ancestral placentals—indeed, the early mammals as a whole—seem to have been small sly animals which were potential flesh-eaters, but were forced to live, owing to their size, on small prey such as insects, grubs and worms, and presumably on some of the softer vegetable materials. Owing to the constant threat of the great reptiles which were their contemporaries, they led, of necessity, lives of timidity and obscurity. This phase of mammalian existence lasted for many millions of years before the dinosaurs became extinct and the mammals were set free. This time was not, however, entirely wasted. It was a time, it seems, of training and preparation, during which advances were made in mental development and in reproductive processes. As a result there had evolved by the end of the Age of Reptiles not only forms on the marsupial level, but highly developed if small placental mammals, ready to take over the surface of the earth.

At the beginning of the Ceñozoic there rapidly developed a great radiation of mammals into a variety of orders. Some fees forms, however, have remained not too distantly removed in structure and habits from their small insectivorous ancestors; these constitute the order Insectivora. The little shrews closely resemble, in habits at least, their remote ancestors; in many regions shrews are exceedingly abundant in woods and meadows, but so shy are their habits that they are almost never seen. Other familiar insectivores are the prickly European hedgehog and the moles, which, with powerful digging limbs, have taken up the pursuit of grubs and worms underground.

Developed from insectivore ancestors is the one group of mammals which has attained true flight—the bats, forming the order Chiroptera. The bat wing differs from that of pterosaurs and birds in that it is a web stiffened by four of the five "fingers." The majority of bats have remained insectivorous in habits;

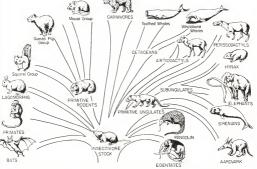


Fig. 44. Diagrammatic family tree of the orders of eutherian (placental) mammals. Separate diagrams (Figs. 45-48) give in more detail the evolution of primates, carnivores, and odd- and even-toed ungu-

however, one major group, abundant in the tropics, consists of relatively large fruit-eaters.

Primates. This order, to which we ourselves belong, was an early offshoot of the insectivores; indeed, so close are the ties that it is an unsettled question as to which of the two orders certain fossil and living forms should be assigned. Primitive mammals are thought to have been to some degree arboreal; this mode of life was emphasized in early primates and appears to have been responsible for the development of many features of importance—general body agility and coordination; the ability to climb by grasping a limb, which has resulted in giving us that most useful of "tools," the hand; the high development of vision, so necessary for arboreal life (with a concomitant reduction in olfaction). Most important of all, the high degree of development of the brain, which is the outstanding character of higher primates, appears to have been closely correlated with the needs and opportunities found in arboreal life.

The tree shrews of the Malay region are so close to the boundary between insectivores and primates that their position is disputed (Fig. 45). Lowest of acknowledged primates are the lemurs, still flourishing today in the isolation of Madagascar and little changed from early Cenozoic ancestors. These are still flouriooted arborat forms, with thick fur, relatively poor eyesight and a nose forming a typical mammal muzzle. A step in advance is represented today by the curious little creature named Tarsius, from the East Indies. The living form is

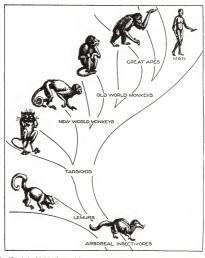


Fig. 45. A simplified family tree of the primates. (From Romer, The Vertebrate Story, University of Chicago Press.)

somewhat specialized in such characters as an elongate ankle region—a hopping adaptation to which it owes its name. But while still lemur-like in many ways, Tarsius shows advances in such features as excellent eyesight and reduction of the nose to a mere button.

The higher general level of primate evolution is that represented by the monkeys, apes and man. Although man may pride himself on mental attainments, anatomic differences between the various members of the group are few, and are mostly matters of proportions of various structures or obvious adaptations—such as the distinctive human features of vertebral posture and hind leg structure associated with upright gait. In all these higher primates the cerebral hemispheres are relatively large, eyesight highly developed, the nose reduced, the hands useful grashing organs. Two distinct groups of monkeys appear to have arisen inde-

pendently from a Tarsius-like stock. One, termed the platyrrhines, is found in South America, where it is represented by a variety of forms such as the common organ-grinder's monkey-the Capuchin-and the little marmosets. (Incidentally, it is only in South American monkeys that a prehensile tail is to be found.) A second group of higher primates—the catarrhines—developed in the Old World. Primitive members are the familiar monkeys and baboons of Africa and Asia. More advanced members are the great apes including the gibbons, the orang-utan, the chimpanzee and the gorilla. All these apes are of relatively large size, in all the tail has been lost, and in the last two forms mentioned the anatomic similarities to man are close indeed, although neither is a human ancestor. The gibbon is an agile arboreal acrobat and the orang is a good traveller in the trees; but arboreal specialization is less marked in the chimpanzee, and some gorillas have become nearly completely terrestrial, although as quadrupeds. Man is essentially a fifth member of this great ape series; he has become a terrestrial biped, but has stamped deeply into his structure features acquired during his long ancestral sojourn in the trees. We do not fully know our own pedigree, but the fossil "man-apes" of South Africa (the australopithecines) structurally bridge the gap between man and his simian relatives.

Carnirores. The insectivores were potential flesh-eaters. With the development of numerous mammals of the more harmless varieties there soon arose from the primitive placental stock varied predaceous types which began the history of the order Carnirora (Fig. 46). Some of the first "experiments" along such lines were relatively ineffective, slow, clumsy, and it would seem, stupid, but more progressive types ancestral to the later carnivores soon evolved. The modern terrestrial carnivores may be essentially divided into two great groups, of which dog and cat are familiar examples, and the weasel tribe and civet group

are, respectively, more primitive members.

The weasels and their close kin, small and short-legged in build and often purely carnivorso in habits, are seemingly primitive members of the general "dog" group (arctoids). But within the weasel family there developed a considerable series of forms variant in habits and diet—badgers, skunks, otters, even a marine member, the sea otter of the Pacific. The dog family developed into terrestrial types, adapted to running down its prey, and is represented today by a series of wolves, jacklis, foxes and other doglike forms. The raceoon is related to the dog stock, but is a persistently arboreal animal with an omnivorous taste in food; there are several American relatives, and the curious panda and giant panda of Asia are allied. The bears are the members of the general dog group which have departed most widely from ancestral conditions; these clumsy fellows have (except for the polar bear) swung far away from flesh-eating to take up a mixed—but mainly herbivorous—diet.

Of the "cat" group of carnivores (acluroids), the civets and their relatives appear to occupy a primitive position comparable to that of the weasel family in the "dog" group. These varied forms are mainly Old World tropical forest dwellers, with which the average reader will not be acquainted; the mongoose is the most familiar representative. The unattractive hyenas are an overgrown offshoot of the civets which have taken up a life of scavenging. The felids form the most highly specialized development in this subgroup of carnivores. The cats are adapted for stalking their prey and making an agile jump on to the victim, rather than running it down as do the dogs, the teeth are highly specialized for stabbing and shearing, and in nature the cats are purely flesh-eating. Most living cut types

—such as the lion, tiger, panther and so forth—are very similar to one another in structure; the extinct sabre-tooths were notable for an exaggerated development of stabbing teeth (cf. Fig. 220, A).

Last of the carnivores to be mentioned are the marine pinnipeds—the various easls, which are fish-caters, and the grotesque walrus, with its digging tusks
and blunt molars for crushing the mussels upon which it feeds. These appear to
have evolved from land carnivores in mid-Tertiary times; in pinnipeds, among
other adaptations, the limbs have been transformed into "flippers"; the hind
limbs, turned backward, replace the reduced tail as a swimming organ.

Ungulates. Notable in Tertiary history has been the development of great series of forms, often of relatively large size, which have assumed an herbivorous mode of existence and developed dentitions with good grinding molars for chewing vegetable food materials. The more advanced forms of this sort have tended to become good running types, with himb elongation, adding an extra joint to the limbs by lengthening the bones of the "palm" and "sole" region of the feet, they have tended to walk on the tips of the toes, which are generally reduced in number. The claws borne by primitive mammals have generally given place to hooves —hence the term 'ungulates' amplied to these herbivores.

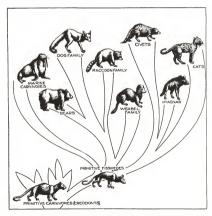


Fig. 46. A simplified family tree of the carnivores. (From Romer, The Vertebrate Story, University of Chicago Press.)

Although the varied ungulate types have developed many common characters, it is far from certain that all ungulate stocks spring from a common source; there has surely been considerable parallelism in their development. The statement, all too often seen in print, that "the ungulate" has such-and-such physiologic or structural features, is valueless unless it is more specifically stated just what type of ungulate is meant; a cow is not improbably as closely related to a lion as to a horse.

Early in the Age of Mammals there rapidly sprang into existence a host of ungulates of varied but archaic types; most passed rapidly out of existence and need not concern us here. The dominant ungulates of later Cenozoic and Recent times belong to two very distinct orders, characterized by the horse and cow the orders Perissodactyla and Artiodactyla, respectively the odd- and even-toed types.

In the Perissodactyla (Fig. 47) the key character has been the early reducino of the toes from five to three, and in the case of the later horses further reduction to a single-toed or monodactyl condition (cf. pp. 168–171). Primitive forms such as little Eohippus (or Hyracotherium), which was not only a "dawn horse" but close to the ancestry of the entire order, had already reached a three-toed condition in the hind foot but in front had lost merely the thumb. Early perissodactyls were browsers, living on relatively soft food materials in forests and glades. In the progressive series of the horses, mid-Tertiary types had occupied the spreading grasslands, developed high-crowned teeth to cope with a diet of grasses and grains and had reduced the toes to three on each foot. With further

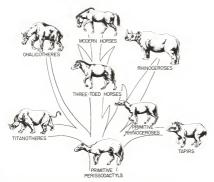


Fig. 47. A simplified family tree of the odd-toed ungulates, the perissodactyls.

approach to the modern genus Equus there was attained a single-toed pattern; the middle toe was the sole survivor. The tapirs of Old and New World tropics are persistent browsers which, although larger, have departed little from the mode of life of early perissodactyls. More divergent among extinct odd-toed ungulates were the large and ungainly borned titanothers and the grotesque chalicotheres, which combined a somewhat horselike body with feet armed with powerful claws (perhaps used for digging tubers). More successful, despite large size and somewhat clumsy build, were the rhinoecroses, which during their history developed hornlike defensive weapons; once common and widespread, they are still represented by a few species in the Old World tropics.

The perissodactyls were very successful in the earlier part of the Age of Mammals, but are now reduced to a relatively few species of three types—horses, tapits, rhinoecroses, Quite in contrast has been the story of the order Artiodactyla (Fig. 48). Rare in the early Tertiary, these even-toed ungulates became increasingly abundant in later times and are widespread today. In these forms toe reduction began with the loss of "thumb" and "big toe," giving a four-

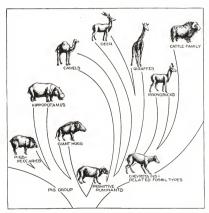


Fig. 48. A simplified family tree of the even-tood ungulates, the artiodactyls. A major cleavage is into the pig group, to which the hippopotamus and extinct giant hogs helong, and the cud-chewing ruminants. The little cherrotains of tropical Africa and southern Asia are close to the ancestry of advanced ruminant types. (From Romer, The Vertebrate Story, University of Chicago Press.)

toed pattern. Among the four, the two side toes tended to reduction or loss, leaving toes three and four to form the so-called "cloven hoof" diagnostic of the group. The pigs of the Old World and the related peccaries of the New are relatively primitive types, omnivorous in habits. The hippopotamus is a lumbering amphibious cousin of the pigs, a vegetarian in diet. The more successful artiodactyls became purely herbivorous, developed a series of grinding cheek teeth with characteristic crescentic cusps (cf. p. 242) and perfected a multi-chambered stomach associated with the cud-chewing habit (rumination, cf. p. 268) for dealing with vegetable foods. The camels, originating in North America, but now surviving in the Old World and (as the llamas) in South America, are relatively primitive cud-chewers. The most advanced artiodactyls are the Pecora-agile, swift-running ungulates, with highly developed ruminating stomachs and with heads generally armed with some kind of horns or antlers. The deer and giraffe are relatively primitive browsers. Much more abundant are the "cow-like" forms, the bovids, most of which have become (parallel to the horses) grass-eating plainsdwellers. Cattle, sheep, and goats are familiar domesticated bovids; for a host of others, mainly inhabitants of the Old World tropics, we have no familiar specific names and tend to lump them as "antelopes." Finally, in this ruminant assemblage we may mention the prong-buck of the western American plains, survivor of a New World group paralleling the true antelopes.

Subungulates. Frequently grouped as the subungulates are a series of orders, probably originating in Africa, which are perhaps best regarded as aberrant offshoots of a primitive ungulate stock. The little hyraxes-order Hyracoidea, the "conies" of Scripture-are animals of rather rabbit-like size and habits, but are definitely hoofed ungulates whose pedigree goes back to the fossil records of the early African Tertiary. They have, however, never progressed structurally to any degree and have never ranged beyond Africa and the eastern Mediterranean region. Strange as it appears, these little forms appear to be related to two other quite divergent groups-the elephants and the sea cows. The Proboscidea (whose name derives from their trunk) are represented today only by the two elephant types proper to Africa and to southern Asia. Their history, however, has been long and varied. The older types are termed mastodons. The most primitive known form, from the Eocene of Egypt, was already large for its day-much the size of a large pig-with chisel-like front teeth and a good set of grinders in the cheek. Later mastodons increased rapidly in size and developed long jaws, with short tusks both above and below. Later the jaws diminished in length, but the upper tusks, in seeming compensation, tended to elongate and eventually there developed the characteristic head pattern of tusks and trunk seen in the modern elephants. Meanwhile, from mid-Tertiary times on, the mastodons had spread widely over Eurasia and eventually over the Americas; in the Ice Age a variety of elephants, most of them termed mammoths, roamed every continent except Australia and South America. Toward the end of the Pleistocene nearly all of the proboscideans vanished. The reasons for the sudden reduction of this seemingly flourishing order of mammals is a mystery, but no more of a mystery than the nearly

To class the sea cows—the manatees and dugongs of the order Sirenia—with the ungulates would appear superficially to be a gross misuse of terms. Hese animals, browsers in shallow waters of the tropical Atlantic and Indian Ocean regions, are purely aquatic beasts, with front limbs transformed into paddles, hind legs reduced to concealed vestiges and the tail re-developed to form a horizontal

simultaneous extinction of a variety of other large mammals as well.

swimming fin. Now relatively rare, they ranged widely over the world for much of the Tertiary. The oldest fossil remains—many from the Eocene of Egypt show a number of resemblances to the most primitive conies and mastodons and add strength to the belief that all three of these curious subungulate groups are varied descendants of some common archaic ungulate ancestor who existed in Africa at the dawn of the Age of Mammals.

Whales. Although both carnivores and subungulates have developed aquatic types, none of these is as highly specialized for marine life as the whales and porpoises which constitute the order Cetacea. Much as in the sirenians, the front legs have been transformed into flippers, the hind legs have vanished, and the tail has become a highly developed swimming organ, with horizontal flukes. As in ichthyosaurs among the reptiles, a dorsal fish-like fin may re-develop and the neck region is shortened, so that a streamlined fusiform fish-like body is reattained. The skull is peculiarly altered, for the external nostrils have moved upward to become the "blowhole" atop the head. Most mammals cannot survive long under water, but the physiology of whales has been so modified that some can remain submerged for the better part of an hour. The greater part of the order, including the porpoises and dolphins and most of the larger whales, are toothed forms which subsist on animal food-fishes, octopi and squids. However, the very largest of the "noble cetaceans," the whalebone whales, live on the smallest of food materials-the small marine organisms that constitute the ocean's plankton. Teeth are here absent, and instead there hang from the roof of the mouth row after row of thin sheets of cornified skin, the whalebone. The fringed edges of the whalebone sheets strain the plankton from the water and the resulting "catch" is licked down by the whale's tongue. The oldest known whales, from the Eocene, were already aquatic types, but less specialized in body and skull and suggestive of a descent from some primitive type of land carnivore.

Edentates. Extremely aberrant in many ways are the members of the order Edentate, mainly South American in distribution and history. The living representatives are the tree sloths, dull, sluggish arboreal leaf-eaters; the long-smouted anteaters; and the armadillos, omnivorous feeders which have a well-developed back armor. Extinct are two further types which attained large size, the glyptodonts, relatives of the armadillos, with a dome-shaped protective "shell" and an armored tail, and the great ground sloths. The anteaters are actually elentations, but the ordinal name is a misnomer for the other forms, which have at least a good cheek-grinding series (although the cananel covering of the teeh is reduced). The group attained its development in South America, but during the Ice Age ground sloths and glyptodonts invaded North America with momentary success. However, only the armadillo has survived in the north; the reason for the extinction of the large edentates is as puzzling as in the case of the mammoths.

We shall mention here two odd types of mammals which in the past were often grouped with the South American edentates, but are now recognized as quite distinct. The aard-vark (Orycteropus) is a grotesque long-snouted African beast; the slender-snouted pangolins (Manis) of the Old World tropics are unique among mammals in that they are completely covered by overlapping borny scales which give them somewhat the appearance of animated pine cones. Both make a living by invading termite nests and are armed with powerful claws. The aard-vark has retained a few peg-like cheek teeth; the pangolin, like its South American anteating analogues, has lost its teeth, useless in this mode of existence. Neither animal has any close relations with any other group; the aard-vark is suspected of

some remote relationship (despite its peculiarities) with the archaic ungulates; there is no clue whatever to pangolin ancestry.

Rodents. Most successful of all mammals from the point of view of both numbers of genera and species and numbers of individuals are the gnawing animals, the order Rodentia. The key character of the group lies in the development of an enlarged pair of front teeth in both upper and lower jaws into an effective chisel-like gnawing apparatus. Rodents have never (we may be thankful) developed into flying forms, nor into marine types; but in almost every known terrestrial habitat rodents are the most flourishing group. Rodents have spread out into a great variety of forms, which are difficult to classify into major subgroups; three "clusters" of forms, however, stand out rather prominently. (1) A relatively small but familiar group is that of the squirrels, prairie dogs, marmots and relatives including, some believe, the beavers. (2) The guinea-pig is representative of a great group which includes most of the rodents of South America. The North American porcupine appears to be of South American origin; the Eurasian porcupine and a few other Old World rodents have been often assigned to this group, but current opinion inclines to a belief that the resemblances are due to parallelism. (3) Most flourishing of rodents are the rats and mice, ubiquitous in distribution; an indication of their versatility is the fact that they include the only terrestrial placentals that were able to reach Australia before the coming of man.

Lagomorphs. The order Lagomorpha is a small one, including almost exclusively the hares and rabbits. They were at one time classed with the rodents because, as in that group, there are chisel-like froat teeth. But there is no other resemblance: furthermore, the lagomorphs have two pairs of upper chisels rather than one. For decades students of recent and fossil mammals have recognized the lack of relationship, but despite this there constantly recur instances in which biologists ignorant of the animal world have described structures or functions

found in the rabbits or hares as characteristic of "the rodent."

On our brief survey of the world of vertebrates we have seen the rise of man groups to prominence, followed by decline to extinction or to a point where there remain today only a few relict types, often aberrant or degenerate. Major success lies currently with the teleosts, the birds and the placental mammals. At the future we can only guess. But, apart from such damage as man may do to himself and his fellow vertebrates by his blundering utilization of major natural forces, it is likely that the progressive teleosts may long dominate the seas, the birds the air, the placentals the surface of the earth. What placentals? We fancy ourselves. But in moments of pessimistic realism one may consider the possibility that the hardy, fecund and versatile rodents may inherit the earth.

# 4

## CELLS AND TISSUES

Although anatomic and physiologic studies of the vertebrate body generally deal with gross structures—organs and organ systems —it must never be forgotten that these structures are composed of tissues, and these in turn of cells, and that the cells are the basal living units from which and by which the entire complex body is built. A knowledge of cell and tissue structure and function is basic in the study of biology; here we shall very briefly review these familiar topics simply as a background for a better understanding of structures of greater complexity with which this work is primarily concerned. The functioning of body organs depends basically upon the activities of the cells of which they are composed; conversely, the varied organ systems are nearly all engaged, directly or indirectly, in furnishing the cells with the materials required for their vital processes and in maintaining them in a suitable environment. Each cell lives it sown life; but each is dependent upon other cells and tissues for its continued existence, and each in turn makes its contribution to the welfare of the total organism.

Chemical Materials. Much of vertebrate structure and function is related to the collection, transformation, and transportation to every cell of the basic chemicals needed to form and maintain its protoplasm and enable it to play its proper part in the work of the body and, again, to the disposal of wastes formed by its activity. In consequence, it is important that we note briefly the major types of chemical molecules concerned in the life processes of cell.

Water, of course, is in bulk the major material concerned. Perhaps threequarters of the content of the average cell is water—a nearly universal solvent, highly useful as a transport medium and one in which chemical reactions can take place; water may itself be utilized in these reactions or may be produced as "metabolic water" as the result of intracellular activity. In the water portion of the protoplasm may be found a variety of ions of inorganic salts, similar for the most part to those present (as noted later) in the extracellular hody fluids, with sodium, chloride, calcium, phosphate, potassium, and sulfate as the more abundant ions.

But it is, of course, the numerous and varied organic compounds that are of overwhelming interest and importance in cell chemistry. Such compounds can CELLS AND TISSUES 81

be variously altered and transformed in animal cells and can be to some degree manufactured by them; but in general they must be ultimately obtained from the plants which manufacture them, using solar energy, from carbon dioxide, water, and nitrates.

A prime feature of organic compounds is the presence of a considerable protrion of atoms of that versatile element carbon, which, in the form of chains or rings, forms their "skeleton." Oxygen and hydrogen are almost as abundant in these compounds; nitrogen, in smaller amounts, completes the quartet of basic organic elements; sulfur and phosphorus are present to a lesser degree, as are "trace" metals.

Simplest of organic compounds are the carbohydrates, which consist of a combination of carbon with bidrogen and oxygen in the proportions of water—mostly in the form of H and OH groups attached to ring-shaped skeletons formed by carbon and oxygen atoms. Simple carbohydrates are the sugars, of which glucose is the common animal type. Sugars may, for compact storage purposes, be combined into long chains as starches, of which glycogen, composed of thousands of glucose units, is the characteristic animal form. Glucose is abundant in typical cells, but is hardly an integral part of their "vital" materials. Rather, it is to be considered as a "fuel," an energy supply for life processes, breaking down, in the presence of oxygen, to form carbon dioxide and water, and yielding energy as it does so.

A second major category of organic compounds is that of the lipids, or failite substances, of which the most familiar are the true fats. These have a monotonous structure—mainly a long chain of carbon atoms, to each of which is tied a pair of hydrogen atoms. A fat consists of three such chains bound together by a molecule of the simple carbohydrate, glycerol (glycerin), Fats, like carbohydrates, appear in the main to be fuel reserves in storage, although certain of them appear to be highly essential for animal tissues. The phospholipids, or phosphorated fats, differ in that but two fatty acids are attached to the glycerol molecule, the third position being occupied by phosphoric acid bound to a nitrogen base. Classed with the lipids as a catchall are various substances, important in vital processes, termed the steroids. These are mainly rather simply constructed molecules, chiefly composed of hydrogen atoms hung on carbon rings. The ubiquitous vertebrate steroid is cholesterol; also in this category are various hormones (cf. Chapter 17).

"Much more "vital" in nature than lipids in general are the proteins, which fulfill many of the most essential functions of living cells. A basic difference from carbohydrates and fats lies in the presence of nitrogen. Protein molecules are giants in the chemical world. They are formed by a compounding of chemical structures simple in nature (but including a nitrogen atom) termed amino acids. Only a score of amino acids are known, but enormous numbers of these building blocks may be combined into chains or networks of almost infinite variety. One common structural shape is that of linkage of a long series of amino acids into a long chain, coiled helix-fashion, termed a polypeptide chain. A special category of proteins is that of the enzymes, ubiquitous and absolutely essential catalysts, which speed up reactions involving organic materials; these are proteins to some of which is attached a small additional compound that may be the active agent.

Certain overwhelmingly important organic molecules belong to a further special category of nitrogen-bearing compounds, the nucleic acids, made up of units called nucleotides. A nucleotide includes phosphoric acid and a simple sugar (ribose or desoxyribose) combined with a nitrogen-bearing base. Simple nucleotides may carry out important functions, notably adenosine triphosphate (ATP), the partial breakdown of which affords a major source of immediate energy in the chemistry of the cell, especially in muscle activity. It is becoming increasingly clear that nucleic acids, formed as long, double helices by the union of successive nucleotides, lie at the very heart of life. One, desovyribonucleic acid (DNA, for short), is abundantly present in the chromosomes of the cell. These molecules, capable of reproducing themselves and seemingly directing the cells metabolic activity, may well be the genes of the geneticist. The molecules of a second, related substance, ribonucleic acid (RNA), appear to act as messengers, carrying the "information" supplied by the DNA molecules to pattern the formation of proteins, including the enzymes.

A final group of special organic molecules essential to the well-being of cells are the vitamins. These do not form a single class of compounds but are, simply, odds and ends of vitally needed materials that the animal itself cannot synthesize. Much of our knowledge of vitamins has been obtained from a study of human dietary deficiencies; but since it is known that, at the far extreme of the spectrum of life, many microorganisms show needs similar to those of man, we can infer that vitamin needs are much the same throughout the vertebrate series.

What materials must be supplied to the cells for the formation of their essential compounds and for the continuous chemical activity that is the essence of the process of living? Oxygen, obviously, is needed in constant supply as an energy source. Water must be available when needed. Inorganic ions may be needed, not only to keep up appropriate salt levels in the cell fluid but also—particularly phosphorus and sulfur ions—for utilization in the building up of organic compounds within the cell. Glucose and fats are required for consumption or storage and the former for use in "manufacture"; amino acids are necessary as building blocks in protein and enzyme synthesis. Needed too are the materials grouped as vitamins.

Returned to the interestitial fluid, and thence to the circulation for disposal, are the wastes from metabolic processes. Carbohydrates and fats, if completely oxidized, are returned as carbon dioxide and surplus metabolic water. More dificult for disposal purposes are the end products of the break-down of proteins and other substances containing nitrogen and such materials as sulfur and phosphorus. Nitrogen leaves the cells as ammonia, NH<sub>3</sub> (this is frequently modified in the liver, to avoid toxic effects, to urea or uric acid). Sulfur leaves the cell as sulfate, phosphorus is eliminated as phosphate (in which form it is always present intracellularly.)

Cell Structure. The general "topography" of a typical cell (Fig. 49) has long been familiar from studies made through the medium of sectioned and appropriately stained materials seen under the lens of the light microscope in recent years the electron microscope has revealed much further detail. Centrally situated in the cell is the nucleus. Here are the chromosome (seen at certain stages in paired series), which have been long known to be the bearers of hereditary characters and strongly suspected of "directing" cell activities. That they have these powers is confirmed by recent studies of the properties of the nucleic acid, DNA, found only in the chromosomes. Also present in the nucleus are quantities of RNA—sometimes in the form of a compact mass known as the nucleo lass. Except at times of division, the nucleus is generally seen to be separated by a membrane from the general cell body. The cell in turn is bounded externally by a definite cell membrane, capable of regulating to some degree the traffic in materials entering or leaving the membrane consists of a few lavers of protein materials entering or leaving the membrane consists of a few lavers of protein

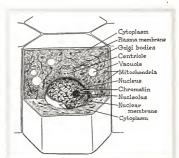


Fig. 49. Schematic drawing of a generalized animal cell. (From Villee, Walker and Smith, General Zoology.)

and lipid molecules. To the cell materials in general the term protoplasm is applied; eytoplasm is a more restricted term, designating the contents of the cell body external to the nucleus. With the ordinary microscope certain formed structures can generally be made out in the cytoplasm. Near the nucleus there are often visible small particles, the centrioles, which play a part in cell division. Scattered through the cytoplasm are numerous little structures, the mitochondria are with the aid of the electron microscope the mitochondria, which appears a mere dots or dashes at ordinary magnification, are seen to have a definite structure as elongate spheroids with a series of internal cross partitions. The mitochondria are centers in which take place much of the chemical activity that supplies energy for the work of the cell. It is in them that sugars and fatty acids are oxidized to yield the energy-rich compound adenosine triphosphate (ATP). Special stains reveal in many cells a reticular apparatus (frequently named after its discoverer, Golzi), a series of tiny vesicles whose function is little understood.

It was long thought that, apart from such structures as those just mentioned, cytoplasm was essentially an amorphous, jelly-like colloid with organic materials in solution in a fluid, watery medium. The development of electron microscopy, however, shows that, on the contrary, the cytoplasm is finely organized with a network of delicate membranes, with vesicles of a more liquid material between them. Scattered along these membranes are small particles, ribosomes, in which protein formation, through the medium of RNA, appears to be active.

Cell Environment; Interstitial Fluid. A major duty owed by the orgame to its cells is to provide the rather rigidly fixed environment, physical and
chemical, needed for their well-being. Although there is considerable variation
from form to form in optimum temperature and permissible departure from it,
the temperatures to which cells of a given animal can be subjected and survive
are usually rather closely defined. In general, "higher" vertebrate groups have
higher optimum cell temperatures, but beyond about 45° C. "heat death" occurs,
apparently through coagulation of proteins. Optimum temperatures are relatively

low in "lower" classes, but the freezing point is, with some possible exceptions, close to the low limit for vertebrate life.

A cell can live and avoid desiccation only if bathed in a watery liquid medium. Such a material, the interstitial (or intercellular) fluid, pervades the body. Water, however, is not enough. The liquid must contain a considerable amount of material in solution; otherwise, through osmotic pressure, swelling and disruption of the cells which it bathes would take place. Still further, vertebrate cells flourish only if the materials in solution-mainly inorganic salts-adhere rather closely to that formula which we find actually present in the normal interstitial fluid. This contains considerable amounts of sodium and chlorine ions, lesser quantities of potassium, calcium and magnesium, small amounts of other elements. It is of interest that, with a few exceptions (lesser amounts of magnesium, absence of sulfate) the materials of the interstitial fluid are similar to those of sea water, although generally much more dilute. The suggestion has been made that this is no accident. It may be that the ancestors of the vertebrates were simple animals bathed in and permeated by the waters of the early Paleozoic ocean; that their cellular physiology was evolved with this type of environment as a basic feature; and that when, as complex organisms, they developed an independent internal environment, this salty interstitial liquid persisted as (so to speak) a remnant of the ancient seas.

The interstitial fluid is in communication with the blood, on the one hand, and with the interior of the cells which it bathes, on the other, through semiper-meable membranes—membranes of organic nature through which water and other small molecules or ions can readily pass, but which block the free exchange of large molecules. The principle of osmosis—interchange through such membranes between liquids differing as to materials in solution—is of importance in many vertebrate structures and is of primary importance with regard to potential exchanges between the cells, the interstitial fluid, and the blood stream.

Epithelia (Fig. 50). The body cells are not isolated entities; they are parts of formed tissues—organized associations of cells generally of similar origins and similar or related functions. In some cases—notably the connective tissues—the aggregation of cells may be a relatively diffuse and amorphous one.

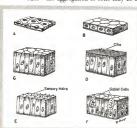


Fig. 50. Types of epithelial tissue. A. Squamous epithelium; B. cuboidal epithelium; C. columnar epithelium; D. ciliated columnar epithelium; E. sensory epithelium (cells from the nasal mucoss); F. glandular epithelium, including mucus-producing goblet cells. (From Villee, Biology.)

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and in the case of cells in the blood stream, the concept that they form a tissue is somewhat of a strain on one's mentality. In many instances, however, the cell association is that termed an epithelium—a regular and compact arrangement of cells in a sheet which borders on one of its aspects the surface of the body or a body cavity. In the embryo, most epithelia are simple and diagrammatic in appearance. Later, however, by thickening and modification, such tissues of epithelial origin as (for example) those of the "gray matter" of the brain or a mass of liver tissue may lose much of their epithelial appearance.

For convenience, there may be used for epithelia various classificatory terms based on the shape of the cells composing them. Spannous colds are flattened types, appearing in section as thin lines; squamous epithelia are characteristic of surfaces through which osmotic exchange is of importance. Caboidal cells are those in which height and width are about equal, so that in section they have a square outline; in columnar cells the height exceeds the width. Embryologically, epithelia often consist at first of a single layer of cells, and this arrangement may continue in the adult as a simple epithelium. When two or more layers are present to form a stratified epithelium, the name applied is derived from the cell type found on its surface. A pseudostratified epithelium is one which is actually but one cell thick but which gives an impression of being stratified, due to the presence, for example, of two types of cells with nuclei, or with greater expansion of the cell bodies, at different depths.

A basement membrane of connective tissue is often present at the base of an epithelium. In some stratified epithelia in which (as in the skin) the surface cells are continually destroyed or lost, they are replaced by division of cells in the deeper part of the epithelium, which may be termed a germinative layer. Various specializations may be present at the surface of an epithelium. Most notable of surface structures are citia, found on a variety of embryonic and adult epithelia of vertebrates as well as invertebrates. These are slender hairlike "organs" which beat in such a fashion as to carry mucus or other materials along in a constant undifrectional stream.

Many authors would restrict the term epithelium to tissues facing the body surface and gut cavity and its derivatives, or to cavities clearly seen to originate from these inner or outer surfaces. When this view is adhered to, alternative terms are used for the lining of cavities formed in secondary fashion in the deeper layers of the body. For example, the term endothelium is generally used for the epithelial material lining the blood vessels.

Non-epithelial Tissues. We have noted that in the case of such structures as the brain and liver, which are clearly seen in the embryo to arise as epithelia, the epithelial appearance is in great measure lost in the adult. Still farther removed in appearance from an epithelium is the striated musculature of the trunk and limbs of the adult. Nevertheless we can, by some stretch of the imagination, conceive of these muscles as epithelia in a broad sense; for (as will be seen in the next chapter) they arise in great measure from compact segmental tissue masses which in Amphiovus, at least, arise as epithelia bounding pouches derived from the gut cavity.

But certain other important body tissues can by no stretch of the imagination be conceived of as epithelia or as of epithelial origin. These are the connective and skeletal tissues and the blood. These tissues arise, as will be noted in the next chapter, from a type of embryonic material known as mesenchyme; the cells of these tissues may be derived from the under surfaces of epithelia, but are themselves never arranged in a compact epithelial fashion. They are, instead, diffusely arranged within a ground substance—a matrix—which they themselves may have created. In the case of the skeleton, the matrix becomes the hard material of the cartilage or bone; in the case of connective tissues, it is gelatinous in nature; in the case of the circulatory system, the matrix is a liquid—the blood plasma.

Glands (Fig. 51). Secretory activity—the production and discharge of huid materials—is characteristic of a variety of cells; those in which secretion is a dominant function are termed gland cells. Frequently their nature is readily seen in microscopic preparations, owing to the presence of granules of material being secreted or of vacuoles filled by secretion in the cell body. The effect of secretion on the cells concerned is variable. In some instances this activity may be carried out constantly without apparent harm to the cell. In other cases periodic discharge of a thick secretion disrupts the outer surface of the cell, but repair takes place. In still other cases, however, (as in the sebaceous glands of mammalian skin) the entire cell is destroved with the discharge of its contents.

In many instances individual gland cells or clusters of cells may occur scattered through the surface of an epithelium which also serves other functions. This is frequently the case with mucous cells, which produce mucus, a thick lubricating material which moistens and protects various membranes. Mucus frequently



Fig. 51. Diagrams of various exocrine gland types. a-g(abore), simple glands; a. tubular; b. coiled tubular; c, alveolar; f, g. branched acinous. Belox, examples of compound glands. In all diagrams, ducts are in double lines, secretory portions in solid black. (From Maximow and Bloom. Histology.)

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accumulates before discharge in the form of large droplets, causing the cells thus distended to be termed goblet cells.

Frequently, however, the secretory cells are not retained on the surface of an epithelium, but are withdrawn from it to form discrete glands. In most cases these glands function by discharging their product through ducts leading outward to the body surface or into some body cavity (as the gut, or urinary or genital ducts); they are hence termed exocrine glands. The withdrawal from the surface serves a variety of purposes; the gland cells are protected from vicissitudes which might be encountered on the general epithelia surface; secretory areas may be increased by folding or pocketing of the glandular epithelium; discharge of secretion may be better controlled.

Some of the various forms which exocrine glands may assume are shown in the accompanying figure. The secretory areas may take the shape of tubules or of rounded pockets—altred in a caini—and may be simple or subdivided. Further, in large glands the duct (which is nonsecretory) may divide, in which case the gland is said to be a compound one and is frequently divided into lobes and lobules.

In contrast to these "normal" glands of exocrine nature, we find in a variety of instances (and in a variety of situations in the body) glands which do not discharge to any surface but, instead, pour their secretions into the blood stream. These are the endocrine glands (Chapter 17). In some instances these can be seen to arise in the embryo from epithelia, and it may be reasonably assumed that they were exocrine in nature in ancestral types. In other cases, however, there is no evidence of such a pedigree, and the phylogenetic origin of many of the endocrines is indeed obscure.

# 5

# THE EARLY DEVELOPMENT OF VERTEBRATES

In later chapters the development of the various organs and tissues will be noted. Here we shall discuss briefly the early developmental history of vertebrates from the egg to the point where the important organ systems have become differentiated and the basic ground plan of the body has been established. In doing so we shall simplify the story in diagrammatic fashion and omit many features of interest to the embryologist.

#### EGG TYPES

The vertebrate egg varies greatly in size from group to group; this size variation (except in teleosts) is correlated with the quantity of yolk present; the amount and distribution of yolk is, in turn, responsible for major differences in developmental patterns. In consequence it is important for us to distinguish between major egg types and to follow through, in parallel fashion, the types of development which result from each condition.

In some eggs—those of Amphioxus and mammals, for example—very little volk is present. Such an egg may be termed oligolecithal.

A second type is that which may be termed mesolecithal; the egg is somewhat larger, containing a moderate amount of yolk which tends to settle into the lower hemisphere. Eggs of this sort are found in amphibians such as the familiar frogs, toads and salamanders, in bony fishes apart from the teleosts, and in lampreys; they are so widespread in lower aquatic forms that it is reasonable to conclude that the mesolecithal egg was characteristic of the ancestral vertebrates.

In the sharklike fishes, on the one hand, and in reptiles and birds on the other, we find eggs of large size—the telolecithal type—with yolk constituting

most of the volume of the cell, and with the relatively small amount of cytoplasm concentrated at one pole. So overwhelming is the yolk mass that in the kitchen the cell body of the hen's egg is simply termed the "yolk," to the neglect of the tiny amount of clear cytoplasm which it contains. In the common modern bony fishes—the teleosts—the egg is sometimes small but is invariably heavily loaded with yolk. It behaves in development somewhat like that of a shark or bird but will not be considered here.

To illustrate the varied patterns seen in the early development of vertebrates we shall select eggs of the three different types discussed above. For an oligolecital egg we shall, in fact, leave the true vertebrates and resort to Amphiosus, a lower chordate relative. The frog or urodele egg is a characteristic mesolecithal type. That of the shark or skate is illustrative of an extremely heavy-yokked telolecithal type, and the bird's egg is similar in nature. We shall, further, note the peculiar early development seen in the mammalian egg. This is tiny and almost devoid of yolk; but mammals have descended from reptiles with large-yolked eggs, and their developmental pattern is one with many 'reminiscences' of that of telolecithal forms. We shall follow each of these types through three successive major processes: (1) cleavage and the formation of a blastual; (2) gastrulation, with laying down of the main body layers; and (3) formation of neural tube and mesodermal structures.

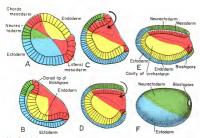


Fig. 32. Gastrulation in Amphicoux. A to E. Median asgittal sections aboving successive stages. (The embryo has been rotated from the original exp gosition to that of the future adult, with head of at left, the former vegetal pole region postero-dorsal.) A. The endoderm cells are a fluttened plate. In R. mendoderm has invagianted and the lateral mesoderm cells, originally widely separated from the not-chordal materials, are moving upward to join them. In C this movement has been mainly accomplished, and the inturning dorsally of chords unaeticals (zeros) continues. D and E. Gastrula formation has been completed, and the embryo (particularly noto-chord and overlying neuroctoderm) is elongating. F. store view of late gastrula, seen from the left. (After Hatschek, Cerfontaine, Cookilia) In this and subsequent figures in this chapter the following colors are used to distinguish germ layers: skin ectoderm, blues moure-chordern, whose moure-chordern, when conversed the control of the con

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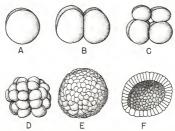


Fig. 53. Cleavage and blastula formation in an oligolecithal egg—that of Amphioxus (cf. Figs. 54 to 656). A, First cleavage; animal pole of uncleaved egg is at top of figure B, Second cleavage, to fourcelled stage. C, Third cleavage; cells of animal hemisphere are somewhat smaller. D, After about two further cleavages. E, Blastula. F, Hemissected blastula, to show segmentation cavity in interior, and sinels-lawered surface. After Certoristine, Conklin.)

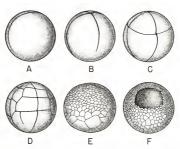


Fig. 5.4. Cleavage and blastala formation in a mesolecithal type of egg found in amphibians. These via figures are comparable to the six in Fig. 53 (cf. also Figs. 55 and 56). A. First cleavage. B. Second cleavage. C. Third—meridosal—cleavage, with smaller cells in animal hemisphere. D. About 36 celled stage, cleavages irregular, but slower and with larger cells in vegetal hemisphere. E. Blastuli, with strong contrast between cells at two original poles. F. Section of blastula, showing segmentation cavity of restricted sixe, blastula a number of cell layers in thickness. Yolky mass at vegetal pole has cleaved, but slowly and into a mass of large cells.

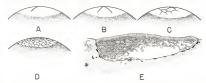


Fig. 5.5. Diagrams to show cleavage and blastuds formation in a large-polked egg, as that of a shark, reptile or bird (cf. Figs. 53 and 54), ln A to B is figured only the animal pole of the egg, containing an area of clear protoplasm on top of the large, inert yolk mass. A to B show cleavage stages comparable to those in A to D of the two preceding figures; the result of cleavage is not a sphere, but a flattened plate of cells. In E is shown, at higher magnification, a section through the formed blastud of a shark. The blastud is a flat plate, a number of cells in thickness, with an irregular segmentation cavity lying below it, but above the unsegmented volk mass E. Enter on Kngffer.)

## CLEAVAGE AND BLASTULA FORMATION

Amphioxus. The seemingly inert and relatively featureless egg of a vertebrate or of Amphioxus contains within itself all the potentialities required for development of the adult, needing only the proper stimulus—normally the trigger action produced by the entrance of the sperm—to set in motion the developmental story. Yolk distribution brings to light even before fertilization on evidence of organization in the egg. Even in a form with as little yolk as Amphioxus, the yolk is slightly more concentrated in a lower "hemisphere," so that we may distinguish an animal pole in the relatively clear cytoplasm above, a regetal

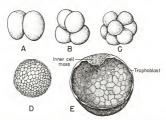


Fig. 5.6. Cleavage and blastula formation in a primate. The small, almost volkless egg cleaves (I of D) in a fishion similar to that of Amphiouxa. The formed blastula (seem in section at E) has a deceptive resemblance to that of Amphiouxa. Actually, however, the thin external sphere is the trophoblast, which forms a connection with the uteries well, and the true blastula is merely the inner cell mass. This is a sheet of cells placed above the internal cavity much as the blastula of a telolecithal egg (Fig. 55, E) is situated atop the yeak mass. (Alber Streeter.)

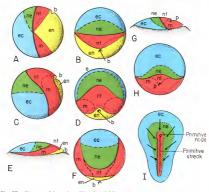


Fig. 57. Diagrams of the surface of blastulae of different types to show the presumptive face of various (cf. Fig. 53, E). C. B. Similar views of an amphiban eng (cf. Fig. 54, E). In these figures the embryo has been totated from the position in which the egg originally ideated to that assumed by the gastrals, the birth is such that the vegetal pale region, originally ventral, has rotated posteriorly, and upward to essentiarily indicated by an identation of the control of the cont

pole in the yolk region below. In many invertebrates the axis connecting these two poles becomes the anteroposterior axis of the body, the vegetal pole becoming the posterior end. In the vertebrates and lower chordates this is not the case. Related to the greater complexity of development, the adult axis in Amphioxus lies about 45 degrees off the egg axis, so that (to put it crudely) the animal pole slants down beneath the prospective chin of the adult, and the vegetal pole slants upward and posteriorly toward the back of the animal.

A first major sequence of events after the entrance of the sperm is the process of cleavage, leading to the stage known as the blastala. In Amphioxus (Fig. 53) the first cleavage is longitudinal, extending from pole to pole (much as one cuts an apple into two portions), and results in the formation of two cells des-

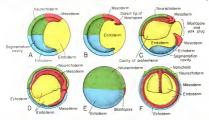


Fig. 38. Gastrulation in an amphibian type of egg. 4 to D are views comparable to A to E of Figure 22. The presence, however, of a large mass of yolk restricts invagination to the extent shows at B the remainder of gastrulation is performed by further growth of the blastopore lips, as indicated for doesal lip larrow in E C. Extrath from the side, E. Transverse section, looking anteried; N can be from C, D and E, the mesoderum folds inward between ectoderum and endoderum (cf. Fig. 67, A, B, D, D), (After Hamburger-)

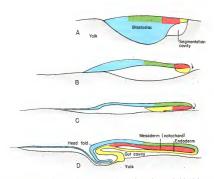


Fig. 59. Longitudinal sections of successive stages in gastrulation of an egg of telelocithal type, as seen in an elasmobranch. Only the disc of the blastula and the neighboring part of the yolk are shown. Anterior end at leth. A, Blastula (d. Fig. 55. E); B, involution of endoderm at posterior end of disc, corresponding to blastopore, C, continued process of inturning of mesoderm; D, mesoderm separated from endoderm, gut eavily formed, open below, roafed by endoderm. A(Bradekrock.)

tined normally to become the right and left halves of the body-here, and probably in vertebrates generally, the median plane of the future body was already established in the unfertilized egg. A second division is likewise longitudinal, the process being similar to that of cutting an apple into quarters. The third division is at right angles to both those preceding—essentially a cut around the equator of the egg, resulting in an eight-celled stage. Each cell resulting from a division of the egg continues to adhere to its neighbors, but nevertheless tends to maintain a spherical shape. In consequence there tends to develop, from this point on, a central cavity inside a sphere of cells-a cavity which becomes increasingly large as division proceeds, and which is known as the segmentation cavity or blastocele. Another feature also begins to be apparent at this time. A cell tends to divide, not through the center of its gross mass, but through the center of its living protoplasm, without regard for such relatively inert materials as volk. We have noted that even in Amphioxus there is a bit more yolk below the equator than above. In consequence the "equatorial" division just mentioned is not exactly through the equator, but slightly above it, and as a result the four lower cells are slightly larger and more volky than those above.

Each of the eight cells divides into two, to form a 16-celled stage; each of the 16 again divides, to give 32 cells. Beyond this point, cleavage proceeds in somewhat similar but less regular fashion and, by geometric progression, a few more cleavages result in the formation of a blastula. This product of segmentation is, in Amphious, a single-layered hollow sphere composed of several hundred cells arranged in a sheet around a central cavity. The cells of the blastula are not too dissimilar from one another, but observation reveals the presence of smaller cells toward the original animal pole and larger and somewhat more volky cells

toward the vegetal pole.

Mesolecithal Eggs. The segmentation of the egg of such a mesolecithal vertebrate as a frog or salamander (Fig. 54) follows essentially the same course as that of Amphioxus, except for modification caused by the presence of a considerable amount of yolk in the vegetal hemisphere. As in Amphioxus the first two divisions are longitudinal, starting at the animal pole, but the presence of masses of inert yolk tends to slow up the cleavage process, so that the second cleavage may be well under way before the first has been completed to the vegetal pole. This tendency for retardation of division in the lower portion of the egg persists throughout the period of cleavage. Further, the third, equatorial division is far from the "equator," because of the disparity in yolk distribution (almost as far north, one might say, as the Tropic of Cancer). In consequence, the cells of the upper ring are far smaller than those below. Because of this unequal division and retardation of cleavage in the vegetal hemisphere, the resulting blastula differs from that of Amphioxus. There is a great disparity between the small cells of the animal part of the sphere (here several layers thick) and a mass of large, volky cells, in part incompletely divided, which make up the vegetal hemisphere and reduce the size of the segmentation cavity.

Telolecithal Eggs. Ålthough the amphibian egg contains a considerable amount of yolk, there is nevertheless a complete cleavage of the egg in blastula formation. In such forms as sharks, reptiles and birds, however, most of the egg such as the blastula formation (Fig. 55) are confined to the small area of clear protoplasm at the animal pole. The result is a disc, which is a number of cells thick, lying above the yolk. The blastula here is a flat sheet, not a sphere. Its margins, bounded all about by yolk, consist of cells which in less yolky eggs would lie in the vegetal pole region, but are here unable to obtain such a position. In cartographic terms, the blastula is a sphere flattened down into a two dimensional "map" on a north polar projection.

Mammals. The early stages in mammalian development (Fig. 56) are quite specialized and unlike those of any other vertebrates. Typical mammals carry the developing young within their bodies and nourish them by materials at first derived from uterine secretions, later from the blood of the mother through the instrumentality of connecting tissues termed the placenta. This is formed through a modification of embryonic membranes found in all amniotes, and many of the developmental processes of mammals are similar to those of a reptile or a bird. Early stages, however, are unique. The mammalian egg needs no yolk and has none; in consequence, it is very tiny, and early cleavage stages (which take place in the oviduct) are very similar to those of Amphioxus. But in such mammals as the primates it is necessary that there rapidly develop an outer sphere of cells to take part in the formation of a placenta when, very shortly, descent to the uterus has occurred. In consequence, the developing blastula soon comes to be composed of two parts: (1) an inner cell mass from which the embryo itself will form and (2) a thin outer sphere of cells, the trophoblast-an embryonic membrane whose function it is to make contact with the maternal tissues of the uterus.

#### GASTRULATION AND GERM LAYER FORMATION

Amphioxus. We have seen as the result of cleavage and blastula formation the development of the egg into an early embryo which consists in most types of a single body layer in the form of a sphere or sheet of cells. In some instances differences in size, pigmentation, or amount of yolk present in different parts of the blastula indicate the differentiation of specific cell areas destined to form one or another major tissue of the later embryo and adult. In other instances a real differentiation is not readily visible, but the future fate of any given area often can be discovered by (for example) applying a stain to cells in the blastula and following the stained area through into later stages of embryonic development. As a result of such observations and experiments it has been found in a considerable number of different chordate types that the future fate of various cell areas is already determined in the blastula stage; "fate maps." of the blastula regions can be drawn, and several of them are given here (Fig. 57, 4-H).

There now begins a series of movements of specific cell areas toward assumption of the position which they will eventually occupy in the later empty and adult. A major step is the process of gastrulation—the transformation of the single-layered sphere or disc of the blastula stage into a two-layered early embryo, with an outer layer of which part corresponds to the skin surface of the adult, and an inner layer, part of which will form the adult gut lining; the opening into the interior is the blastogore.

In Amphioxus gastrulation appears, deceptively, to be a simple process, meeting the folding of a sphere into a double-layered hemisphere, with skin outside and gut cavity within (Fig. 52). In such primitive metazoans as the coelenterates this situation actually holds true. All the cells of the original animal hemisphere, which form the outer surface of the coelenterate gastrula, constitute the ectoderm, or outer germ layer of the late embryo and adult; the inner cells are

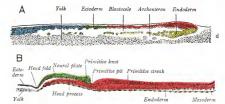


Fig. 60. Two successive longitudinal sections of hird embryon at successive stages to show gastrula tion. A. Figure comparable to the shart, of Figure 59, B, but the endoderm is delaminating rather than involuting posteriorly to form a roof to the archestron. B, Later stage, comparable to Figure 57, L; from the primitive pit lackward, cells are turning down inward from the surface (in the plane of the paper) and rolling laterally to form typical mesoderm, and are moving forward from the pit to form the notochord ("bead process").



Fig. 61. A cross section of the primitive streak at the stage shown in Figures 57, I and 60, B. Mesoderm, as indicated by arrows, is rolling medially, downward in the primitive streak, and then outward laterally on either side; above, the presumptive neural ectoderm is moving inward toward the midline. (After R. Bellairs, in Marshall, Biology and Comparative Physiology of Birds, Academic Press.)

the endoderm, or inner germ layer forming the gut. In the chordates, however, gastrulation is no such simple process. The chordate body is a complex structure. The body materials of the simple coelenterate cup would produce in a chordate little more than the superficial part of the skin and the inner liming of the digestive tract and its appendages. There is needed a special area of the superficial ectodermal layer for the formation of the complicated nervous system, a neuroctoderm. Here must be formed the materials of the third major germ layer, the mesoderm, which constitutes the greater part of the bulk of the chordate body. Still further, there is needed a distinctive mid-dorsal area of mesoderm, the chordamesoderm, which forms the notochord and is of especial importance in bringing about by induction the development of the nervous system.

All these areas are already laid out in Amphioxus in the blastula stage and are involved in the process of gastralation (Fig. 57. d. B). As gastralation begins, the large yolky cells at the vegetal pole, which are to become the endoderm, form a flat plate and then bend inverted at the ventral rim of the forming blastopers. Above, a sheet of chordamesoderm cells rolls inward over the dorsal lip of the blastopore and pushes forward internally, lengthening in the process and tending to lengthen somewhat the gastrula as a whole. With the infolding of this tissue, the potential neurectoderm comes to occupy a large area on the dorsal surface anterior to the blastopore. On either margin of the blastopore, between chorda-anterior to the blastopore. On either margin of the blastopore, the total contents of the blastopore.

mesoderm above and endoderm below, cell masses of the mesoderm proper stream in, forward and upward, and align themselves in a sheet on either side of the chordamesoderm.

When gastrulation has been completed, we find the embryo forming a somewhat elongated spheroid, with the only entrance to its interior the posteriorly placed blastopore, now reduced in size. On the outer surface, the future skin ectoderm forms the ventral epithelial covering; the neuretoderm the more posteriorsal area. Internally the endoderm occupies an area essentially comparable to that of the skin ectoderm on the outer surface; farther dorsally and posteriorly is the mesodermal area, with the chordamesoderm occupying a mid-dorsal position along the roof of the archenteron.

Although not properly a part of gastrulation, the next stage in the development of the mesoderm in Amphiovus will be described at this point; this is the formation of mesodermal pouches (Figs. 65, 66). Of the mesoderm, that part lying along the dorsal midline of the archenteron roof "rounds up" to form the

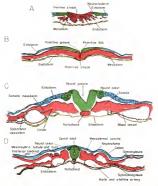


Fig. 62. Cross sections of chick embryos to show successive stages in development of mesodern and neural tube. A, Stage in which the inturning of mesodern in the primitive streak has begun. B, The mesodern has spread widely on cither side between extodern and endodern, but has not differentiated in turture (c.H. 19. 61). C. The celonh as begun to appear, splitting the lateral part of the mesodern to outer—somatic—and inner—spharchaic—parts. Centrally, the notechood has separated from the remainder of the methodern, and search folds and creats are appearing on exhibit side of a neural grower. emister of the control of the stream of the control of the control

notochord. The remainder folds outward on either side to form a pair of longitudinal grooves. Beginning anteriorly, these grooves pinch off a segmental series of pouches, the mesodermal somites. The cavities of the somites, originally continuous with the cavity of the primitive gut, are destined to form the celom; the walls later differentiate into mesodermal tissues. As these pouches but off, the endoderm extends upward internal to them and across beneath the notochord to form a continuous definitive gut lining. This pouch type of mesoderm formation is highly comparable to the process seen in acorn worms and echinoderms and is a prime basis for the belief that chordates are related to the echinoderm phylum.

Mesolecithal Types (Figs. 57, C, Dr. 58; 67, A. B., p. 104). In such types as frogs and urodeles, gastrulation takes place in a fashion fairly similar to that of Amphioxus, but there are modifications. At the beginning of gastrulation the blastula "tries" (so to speak) to infold itself; a surface furrow forms at a point corresponding to the dorsal lip of the Amphioxus blastopore, and materials stream inward at this point. But it is physically impossible to infold the whole mass of yolky materials of the vegetal hemisphere in this fashion, and further gastrulation is effected by continued growth of the blastopore lips and inrolling of surface materials at these lips. Eventually a double hemisphere is formed which is fairly comparable to the Amphioxus gastrula. There is, however, a diference in the way in which the mesoderm develops. Pouch formation is suppressed, instead, the infolded mesoderm pushes out between ectoderm and endoderm as a sheet of tissue which eventually reaches the ventral midline; it is only later that segmental conditions and celonic cavities appear.

Elasmobranchs (Fig. 59). Obviously, typical gastrulation cannot occur in the blastula of a telolecithal type, which is merely a flat sheet of cells, not a sphere; however, the process is basically similar to that of Amphioxus or an amobibian.

In normal gastrulation a primary event should be the formation of an endoderm beneath the ectoderm; this should be accomplished, in part at least, by an inrolling of cells at the blastopore lips, particularly the dorsal lip. But where are the blastopore lips in a flat plate? The most reasonable answer is that they lie at the margins of the plate, and the dorsal lip, the most active area, should lie at the posterior end of the forming embryo. In a shark embryo a center of activity at one part of the disc margin can safely be regarded as the dorsal lip region (Fig. 71, A, p. 106). Here there is a rapid overgrowth and inturning of tissue (Fig. 59, B. C) which spreads forward beneath the disc to transform it into a two-layered, flattened equivalent of a gastrula. Skin ectoderm and neurectoderm lie on the surface; beneath is endoderm, with the mesoderm presently expanding between ectoderm and endoderm as in an amphibian. But there still remain differences from the mesolecithal type because of the disc shape. The endoderm does not a first form a complete gut tube, but is merely spread out flat over the yolk surface; the embryo is, so to speak, unbuttoned ventrally.

Repitles and Birds [Figs. 60, 61, 62]. In egg-laying amniotes—reptiles and birds—the blastula is a flat disc comparable to that of a shark, but gastrulation is still further specialized in nature. Here there is no inrolling of endoderm; instead, this body layer is formed by delamination—the splitting off of a deep layer of cells from the under surface of the blastodisc [Fig. 60, 4). Mesoderm, on the other hand, does roll inward through a blastopore; but this blastopore is a highly modified structure, the primitire streak [Figs. 57, 1: 72, B. p. 107]. This consists of a pair of longitudinal ridges with a groove between them and a

pit at the front end of the groove. On the dorsal surface of the disc there is a steady movement of cells into the margins of the primitive streak. In its walls these cells move downward and then fan outward to interpose themselves between ectoderm and endoderm (Figs. 60, B; 61, 62). Anteriorly the central part of the introlled cells forms the notochord. Laterally the material moves outward to form the somites and other mesodermal structures. As infolding of mesoderm is completed, the primitive streak becomes reduced and vanishes; neurectoderm has moved centrally to occupy its old midline position.

Mammals (Fig. 63, C). Gastrula formation in mammals is a unique process. In later stages the mammal embryo comes to be identical in major respects with its anniote relatives, but until gastrulation is completed, it is still quite atypical; it has not yet recovered, so to speak, from its early vagaries. The details of gastrulation vary among mammalian groups; described here is that characteristic of primates.

The blastula, we have seen, consisted of an external sheet of cells which made contact with the utreine tissues, and an inner cell mass. In this latter presently appear, above and below, cavities which expand to leave between them a flat, two-layered plate of cells. The upper cavity, lined with ectoderm, is that of the amnion; the lower is a yolk sae with an endodermal lining. The cavities and the materials lining them are parts of the amniote membrane system described later, the two-layered plate between them is a blastodise, in which the embryo is to arise. Since the under surface of the disc is endodermal, the first act of gastrulation is already accomplished. The remainder of the process is the same as that we have seen in a bird or reptile—the development of a primitive streak and the inrolling of mesodermal materials along its margins (Fig. 73, 4, p. 107).

#### NEURAL TUBE AND MESODERM DEVELOPMENT

The Neural Tube. Following the completion of gastrulation, with the placing in proper relation to one another of the major tissues of the body, at stages in organ formation bring the embryo to a stage termed the neurala. Prominent on the outer surface is the formation of a neural tube, its development "induced" by the presence of the notochord beneath it.

In Amphioxus the neurectoderm occupies a large oval area on the upper and back surface of the gastrula (Fig. 52, E, F). Presently there is an upward folding of the lateral margins of this area. In Amphioxus (not in true vertebrates) skin ectoderm and neurectoderm separate as the folds form. The ectoderm margins from the two sides grow medially over the neural region and finally meet to form a complete layer of "skin" over the top of the body. Meanwhile, the lateral margins of the neurectoderm roll upward, meet, and form a neural tube (Fig. 65). For some time the anterior end remains open as a neuropore. Posteriorly there is a curious situation in that the neural folds close over the blastopore but leave the hind end of the gut in communication with the cavity of the neural tube by way of a neurenteric canal (Fig. 66). In later development, as the tail sprouts out, this canal closes.

Most vertebrates show a type of neural tube development contrasting with that of Amphioxus in that the neural folds never completely separate from the ectoderm proper, but a similar end result is obtained (Figs. 62, C, D; 64, 70, B; 72, C). During the folding process, the folds form high neural creats on either side, from which masses of cells are pinched off into the interior. Some of these

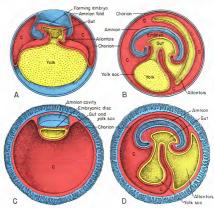


Fig. 63. A, B, Formation of embryonic membranes in repilic or bird. Anterior end at left. A, an early stage. The embryon has been fifted somewhat of the volk, but gut cavity proper and yolk as are broadly connected. Volk as incompletely formed, annion folds and chorion incomplete, allantois harryl indicated B. Lates stage, embryonic membranes formed and yolk already partially preduced, C, D, Comparable views of mammalian type of development as seen in primates. C, Stage beyond the blastonic seen in Figure 56, E. The inner cell mass has guilt ventrally to produce a gat early—constituting the major act of gastrulation—and split dorsally to produce an amnion cavity. Between the two existinct the representations in which primitive streak formation occurs much as in a repilic or bird. Mesoderm has already appeared, and chorionic villi are establishing connections with the surrounding uteritie vall. D. Later stage in mammalian development, corresponding to B, C colonic circle in the contract of t

cells form nervous structures; others, as noted in later chapters, have a varied history. In the head region still other future nervous system elements and sensory structures may arise as placodes—thickenings of the embryonic ectoderm lateral to the neural tube region, which detach themselves from the under surface of the future skin.

Mesoderm Development. The mesoderm forms the greater part of the bulk of the body. Apart from the brain and spinal cord, the ectoderm forms little but the superficial portion of the skin. Except for a mass of liver and pancreas tissue, the endoderm forms little but a thin film of epithelium lining the gut. Practically all the rest of the body is derived from the mesoderm—muscles, connective tissues, skeleton, circulatory, urinary and genital tissues. If comparison

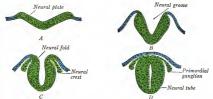


Fig. 64. Formation of the neural tube and crest as seen in a typical vertebrate (mammal); a series of transverse sections at successive embryonic stages. (From Arey.)

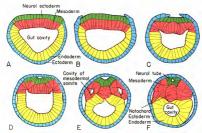


Fig. 65. A series of cross sections to show formation of mesodermal pouches and neural tube in Amphiorus. (Sections E, F somewhat diagrammatic, since the somites of the two sides are alternating in position.) (After Cerfortains.)

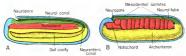


Fig. 66. Amphioxus embryos at a stage in which the neural tube has formed and mesoderm is differentiating. A. Sagittal section. B. Longitudinal view with skin ectoderm sectioned medially, but internal structures preserved intact. (After Cerfontaine and Coaklin.)

be made with a house, the ectoderm corresponds to the paint on the outside and the wiring system; the endoderm to the floor varrish, wall paper and perhaps the kitchen stove. All the rest—frame, plumbing, sheathing, even the floor boards, lath and plaster—is comparable to the mesoderm derivatives.

The nonchord is sometimes described as a structure discrete from the major germ layers. The chordamesoderm is here considered as a part of the mesoderm, but one which becomes distinct at a very early stage as a longitudinal band of cells lying along the roof of the primitive gut. This rapidly rounds up in section to gain its characteristic as an elongate cylinder (Figs. 62, C, D, 65, C–F; 66, 69). In higher vertebrates it is reduced or absent in the adults but in every case it is prominent for a long period of embryonic development. It is of primary importance in that its presence is the factor which "induces" the overlying tissues to form the neural tube.

Apart from the notochord, the mesoderm forms in Amphioxus, as noted earlier, a paired series of somites, each containing a celomic cavity (Figs. 65, 66). In true vertebrates there is a marked modification of this pattern. There is no segmentation of the mesoderm at first, nor any initial development of a celomic cavity, the mesoderm pushing outward on either side as a solid sheet. In mesolecithal eggs the mesoderm of either side grows as a hemicylinder, following the curve of the hody downward and then inward to the midventral line of the belly (Figs. 58, 67, A, B, 69). In telolecithal forms and in mammals, the mesoderm spreads out laterally in the flattened embryonic disc (Fig. 62, A, B), and is continued in amniotes outward into the extra-embryonic membranes; it is only at a late stage that the body develops an under surface, allowing the two mesoderm sheets to meet ventrally.

There presently appears, in all vertebrates, a differentiation of the mesodeterm from the dorsal midline outward into three divisions, each extending the length of the trunk. Next to the neural tube and notochord thickened masses of mesoderm form on either side a series of mesodermal somites (Figs. 62, C, D: 67, C, C, D, C, T, C, D, comparable to the somites of Amphitoxus. These are the first indications of true segmentation in the vertebrate body, and it appears that (apart from the independently derived serial arrangement of the gill structures) the segmentation seen in other vertebrate organs is due to the influence of the mesodermal somites.

Soon differentiation appears within each somite (Fig. 68). There is a great proliferation, from its ventral medial corner, of cells which from an area of loose embryonic tissue of the type termed mesenchyme. This expands around the nerve cord and notochord and forms much of the axial skeletal structures; in relation to this, the part of the somite concerned is termed the selectatome. The external layer of the somite likewise disintegrates; its cells appear to take part in the formation of the connective tissues of the skin, and it is hence termed the dematome. After loss of these two areas, the remaining portion of the somite, the myotome, differentiates to form the axial musculature.

Ventral or lateral to the somites, a relatively narrow region of the mesoderm develops in the trunk into the nephrogenic tissue, from which form the kidney tubules and their ducts, and the deeper tissues of the gonads as well. This region may develop as an unbroken longitudinal band, but in some cases forms a series of small segmental structures, the nephrotomes (Figs. 62, D. 67, C.; 269, p. 282),

Beyond the nephrogenic region, extending ventrally or laterally according to the mode of development, is a great sheet of mesoderm, the *lateral plate* (Fig. 67, C). This is unsegmented (except in cyclostomes). At first it is a solid sheet of tissue; later, however, it cleaves, and the celomic cavity, which in adult life surrounds most of the viscera, develops within it (Fig. 62, C, D). The mesoderm external to the celom, plus the adjacent ectoderm, is termed the somatopleure; the inner mesodermal layer plus endoderm is the splanchnopleure.

During much of embryonic development there exist, between the epithelia and tissue masses of the major organs, relatively empty spaces filled with fluid. Scattered through these spaces is a diffused network of star-shaped cells which compose the mesenchyme, the embryonic connective issue. Much of this is formed by proliferation from the sources, but increments are added from the lateral plate. Both these areas are mesodermal in origin, and mesenchyme is thus a characteristic product of this germ layer. But the ectoderm, as noted elsewhere, and, it seems, the endoderm may also produce tissues of this sort; mesenchyme production is not confined to a single germ layer.

The mesenchyme is a most versatile tissue. It gives rise in the adult not only to connective tissue, but to the skeleton, the entire circulatory system and even much of the musculature.

### BODY FORM AND EMBRYONIC MEMBRANES

Amphioxus and Louer Fertebrates. By the attainment of the neural stage just described, the embryo has laid the foundations for the development of the major organ systems. Their further history will be considered in future chapters. In consequence, we shall not here carry onward in any detail the further development of the embryo; we shall merely describe in brief fashion the gradual assumption of definitive body shape and the nature of the embryonic membranes which are important in the development of large-volked eggs.

At the neurula stage the Amphicoxus embryo had the form of a rather short cylinder. Superficially the remainder of the story is one of body elongation, particularly the budding out posteriorly of the tail, into which neural canal, notochord and somites continue, while anteriorly there develop a mouth and a complex gill structure.

In mesolecithal egg types the neurula is likewise a stubby spheroid, with a rapidly developing nervous system dorsally and ventrally a belly bulging with yolk. With brain growth there is a major development of the head region; posteriorly there is a major development of a tail, much as in Amphioxus, and it is not long before a body shape recognizable in terms of the adult is attained (Fig. 70).

In sharklike fishes (Fig. 71) the neurula is little more than a pancakeshaped plate atop the massive yolk, with its midline marked by the developing neural tube. With brain growth, the anterior end of the body lifts off the plate, as does the posterior end with tail development. Beneath, the body begins to round of from the yolk, to which it still connects by a stalk containing an extension of the gut cavity. Meanwhile the endoderm (covered externally by thin sheets of ectoderm and mesoderm) has continued, manfully, to grow over the surface of the yolk, which is presently enclosed in a yolk sac. The yolk is gradually digested and absorbed, and the sac dwindles and disappears.

Reptiles and Birds. The reptile or bird egg is laid on land, and in consequence these amniotes need further adaptations for embryonic existence in the medium of air rather than water. In addition to a protective shell there develops

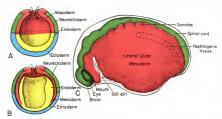


Fig. 67. Mesoderm formation in an amphilian, A. Section of a urodele gastrala, cut transvenedy the through the blastyopers, showing involution of mesoderm into the lateral sulfs of the archenteror. This is essentially similar to the situation in Amphicous at the stage of Figure S2, C or D, B. Later stage the mesoderm, instead of forming holdow pockets, as in Amphicous (Fig. 65), attains its intermediate position by pushing downward and forward between ectoderm and endoderm. C, A later embryo of an anphilian, after the neutral tube is formed, seen in side view the skin has been removed. The meant forms a long, continuous where to either side of the hody. The dorsal part is beginning to subdivide into somities. The part of the mesoderm which will later from takinget ulse part is beginning to subdivide into somities. The part of the mesoderm which will later from takinget ulse is being broken up anteriorly by the formation of gill clefts. (A and B after Hamburger; C after Adelman).

a series of membranes which afford the embryo protection and aid its metabolic activities (Fig. 63, A, B, p. 100). A yolk sac is formed much like that of sharks, but before this has gone far in its development further membranes arise, formed of either ectoderm or endoderm backed by mesodermal tissue. Folds of ectoderm grow upward to form a closed liquid-filled sac, the amnion, in which the embryo may develop in a miniature replica of its ancestral pond. Externally this ectodermal sheet expands to enclose the entire set of embryonic structures in a protective membrane, the chorion. Later, a third new membrane develops, this time as an outpushing from the endoderm near the posterior end of the gut tube. This rapidly expands to form a large sac, the allantois. Its cavity acts as an embryonic bladder; much more important, however, is its function as a breathing organ. The combined chorionic and allantoic membranes operate as a lung surface for gas exchange with the air through the porous shell, and the allantoic stalk is richly supplied with blood vessels to aid in this breathing function. With these membranes formed, the embryo takes shape and grows within the expanding cavity of the amnion (Figs. 63, B; 72, C, D).

Mammals (Figs. 63, C, D; 73, 74). We have noted the precocious development in such mammals as higher primates of an outer ring of cells, the trophoblast, and, a little later, of epithelia lining cavities both above and below the
blastodisc from which the embryo forms. Except that it is not until some time
later that these membranes are reinforced by mesodermal tissue, they are exactly
equivalent to chorion, amnion and yolk sac, respectively. Amnion and yolk sac
develop much as in repitles and birds despite the fact that the yolk sac is yolkless. The final member of the amniote membrane series, the allantois, grows out

Fig. 68. Hemisection through a mammalian embryo to show the subdivision of the somite into mystome, dermatome, and selerotome. Arrows show directions in which mesenchyme grows from selerotome to form vertebra and rib. The small notochord is prosent and the small notochord is proabove the aorta, and part of the gut wall is shown below that large vessel. (From Arev.)



somewhat later from the posterior end of the gut to underlie the chorion. With growth of the embryo and expansion of the amniotic cavity around it, yolk stalk and allantoic stalk come to be connected with the body only as components of a narrow umbilical cord.

The major difference between a placental mammal and its anniote relatives is the development of a placenta which replaces the embryonic lung of reptiles and birds. As in those groups the outer surface of the allantois fuses with the other and the allantois stake is richly supplied with blood vessels. The material transported by these vessels, however, is not merely oxygen but the entire food supply for the embryo. The outer surface of the chorion becomes intimately connected with the tissues of the uterine walls, usually by finger-like processes (vilil); in these conjoined placental tissues there takes place exchange of materials between the closely apposed blood vessels of mother and young.

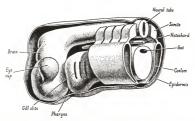


Fig. 69. Stereogram of the front part of an embryo (particularly of a mesolecithal type) after partial differentiation of mesodermal components and nervous system. (After Waddington, Principles of Embryology, George Allen and Unwin.)



Fig. 70. Development of body form in a mesolecithal egg type—the urodele Necturus (the mad pappy).
A. Late gastrula, seen from above, head end at top. B., Neural folds forming. C. View from left side.
neural tube formed, brain bulging upward above see partly filled with yolk. D. Head and trunk taking shape dorsally. E. F. Steps in reduction of yolk-filled belly sac and assumption of normal form. External galls and eve appear in E, limbs in F. (After Keitled).

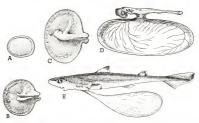


Fig. 71. Development of body form in a shark. A to C are dorsal views of the cellular disc from which the embryo forms, the underlying olds is omitted in these figures. A, The embryonic disc at gastrulation; the endoderm is rolling under at the thickened posterior and lateral margins (cf. Fig. 59, B, p. 199). B. The disc is enlarging, and the neural folds are developing on the upper surfare. C. The neural folds are closed except at the growing posterior end; the body of the embryo is lifting off the volid. and bear depoin and somites are visible. B. The yolks acis completely formed and the embryo connected with it by a stalk; eyes and gill slits are visible. E. Nearly normal shape has developed except for retention of a relatively small yolk size. (After Zeiger, Dean.)

Larrae. In vertebrates with a large yolk, development proceeds rapidly toward adult structure; the young, at birth, is essentially a sturyl little replica of the adult, soon capable of making a living in the fashion of its elders. Not so in many water-dwelling lower vertebrates in which the yolk supply is limited—lampreys, many bony fishes, amphibians. The young, when hatched, is liable to dangers resultant from tiny size and may be incapable of taking up adult feeding habits. In consequence there is often a larnal stage interjected into the life his-

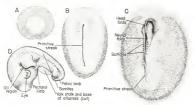


Fig. 72. Some stages in numioto development as seen in reptile or hird. A, Small germinal disc situated on the upper surface of the yolk. B, Formation of primitive streak and elongation of germ disc (E, Figs. 57. I, 60 B, 61, and 62). C. The embryo is enlarging to overn more of wolk; the head region is lifting off the yolk surface, neutral folds and somites are appearing; the primitive streak, now relative small, is still active in formation to posterior part of both O, Side view of a considerably later stage, comparable to Figure 63, B. The embryo is separated from the yolk except by a stalk (cut). Many head and body structures are formed, and links bads are appearing. (B and C after Houttner.)

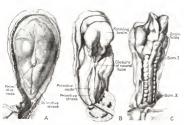


Fig. 73. A series of early human embryon, to illustrate stages in mammalian development. All three are dorsal views of the embryon, with the embryonic membranes cut away. A Primitive streak stage, comparable to Figure 72. B, for a hird or reptile. B, Later stage in which the primitive streak is just? In derive posteriorly, but the nearal tube is forming more antierroly. This stage is comparable to Figure 72. C, for the shark, not quie so advanced as Figure 72. C, for the bird. C, More advanced stage, with near at tube nearly completely closed and somite formingious need hadroned. (Mer Busser, West, Corner.)

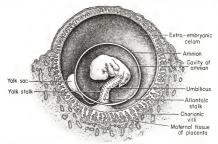


Fig. 74. Diagram to show the development of a primate embryo inside its membranes. The stage represented is one at which the embryo, though well formed, is still of small size.

tory, during which the young animal leads a life quite different from that of the adult and may have specialized anatomic structures adapting it to this life; the frog tadpole and the ammocoete larva of a lamprey are familiar examples. With growth, larval features are lost and adult habits and structures assumed—the process of metamorphosis.

Regeneration. In earlier sections we have more or less tacitly assumed that organs and tissues once formed are permanent. But this is far from being universally the case, even under normal conditions—such structures as hair, feathers, epidermal cells of the skin, blood cells, for example, are normally lost or destroyed and replaced, so that developmental processes of a sort may go on throughout life. Further, when accident or disease causes destruction of tissues there are in every vertebrate certain potentialities of replacement. Even in mammals, which are not notable for regenerative powers, large areas of skin may be renewed, and destroyed liver tissues may be regrown. At the other extreme, urodeless show exceptional regenerative powers, and even a complete limb may be regrown in the sessifial details from an amputated stump.

### DEVELOPMENTAL MECHANICS

In the earlier sections of this chapter we have given a description of the orderly series of events which take place during the development of a vertebrate but have said little as to the "why?" of these processes. The answer to this question is a major interest of embryologists today. The development of the individual from the seemingly simple egg to complex adult is a mirracle so common that we regard it as commonplace. When some accident occurs in this usually well-regulated process, we tend to be puzzled or disturbed over the abnormality that

results. Rather, we should marvel that the process of development normally proceeds so effectively. The mechanisms of development are in most regards still a mystery, and the solution of the chemical and physical problems involved is the chief concern of modern embryology.

Environment has, obviously, a major effect upon the course of development, but this course is mainly set internally. Hereditary factors carried by the chromosomes can be considered basically responsible for the direction of the developmental pattern—particularly those from the female parent, for those from the male, entering with the sperm, appear to be effective only at a relatively late stage in development. The egg, even before sperm entrance, is already "organized" in certain regards, ready when stimulated by sperm entrance to proceed toward a determined goal.

As cell division begins and continues, regional differences appear. In some invertebrate groups the egg organization is so fixed at a very early stage in cleavage, or even before cleavage, that each cell is destined to form one particular part of the adult and can form no other. In vertebrates the early pattern is less rigid; nevertheless, every embryonic cell or region sooner or later loses its original broad capacities and becomes increasingly limited to a more and more narrow range of possibilities. One can mark out at the blastula stage areas which under normal conditions are to become specific germ layers or major organs in the adult (Fig. 57, p. 92). But at this time the cells concerned are not yet highly restricted in their potentialities. If, for example, we exchange bits of tissue at the blastula stage of a urodele between future skin and spinal cord areas, the transplants are capable of following the fate of their new locations. But by about the end of gastrulation these two areas are irrevocably determined as to their general fate; skin ectoderm remains such if transplanted, neural tube tissue will develop as such if placed in the skin. It is as if each cell passed along a series of everbranching pathways; at each fork it must take one path or the other, with its future possible goals becoming more and more narrowly restricted.

This progressive determination appears to be induced through a variety of influences. Cells may be influenced by their topographic position in a "field" in which specific processes are occurring, or differentiation may be evoked by the presence of adjacent tissues or structures. For example, the formation of the neural tube is influenced by the presence of the chordane-soderm beneath it, and at a later stage of development, the formation of an eye lens is dependent in certain cases on the presence of any eye vesicle (cf. Chapter 15). The competence to respond to such chemical or physical influences may be qualified by the degree of histological or chemical specialization already undergone by the cells or tissue concerned, the changes induced may be further histological differentiation of the cells concerned, regional differentiation of special tissues, or the formation of definite organ structures.

### ONTOGENY AND PHYLOGENY

In the early days of embryologic study it was noticed that animals vastly different as adults are similar in structure and appearance as embryos and that the embryos of 'higher' vertebrates often exhibit conditions similar to those seen in the adults of "lower" groups. From such observations came the idea of a biogenetic "law" which proclaimed that individual development—ontogeny—repeated the history of the race—phylogeny; that an animal in its development climbs its own family tree, successive embryonic stages representing the adult stages of ancestral tyees.

This "law" was for decades an important stimulus to embryologic work and in the study of homology. But further consideration shows that it is only a half truth. A mammalian embryo at an early stage is fishlike in many regards, as, for example, in the presence of prominent "gills" which are later reduced or lost. But there is actually little resemblance to an adult fish, for the gill pouches do not open to the surface or develop gill membranes. It is the fish embryo, not the adult fish, which the mammal resemblance between tends to be a conservative process, for departure from the old, tried and true methods will usually result in failure and death. In consequence, the mode of development of an animal may follow well along that which its ancestors pursued, and only toward the end it may diverge to attain an adult condition quite different from the original goal. Ontogeny repeats many important stages in the developmental pattern of ancestral forms. It is especially likely to repeat them if they are structurally or functionally useful in the derived twoes own development.

It must, however, be kept in mind that embryos and larvae as well as adults must be adapted to the environment in which they five, and in consequence, many structures found in growth stages may never have been present in any adult ancestor. For example, no ancestral shark or aminote ever dragged beneath his body a yolk sac such as is present in the embryo, and it is improbable that the feathery external gills of a larval salamander were ever normally present in an adult fish ancestor. Further, despite the general conservative nature of developmental processes, there may occur striking modifications in the sequence of embryonic events, presumably related to powerful adaptive requirements in embryonic life. A notable example is the method of development of embryonic membranes in manmals. The ancestral method seems surely that present in reptiles and birds. The mammals attain the same end results, but have markedly changed the pattern of their development because of the need for rapid formation of a placenta.

#### THE GERM LAYERS

The theory of the germ layers was an early and most fruitful concept in the study of embryology. In the early embryo, ectoderm and endoderm may be distinguished as inner and outer body layers comparable to those which alone constitute the entire body of a coelenterate; soon there is developed a third, intermediate layer from which, in all animals above the coelenterate level, much of the substance of the body is formed. We have in this chapter adhered to this germ layer concept, although emphasizing the early separation between skin and neural portions of the ectoderm and the distinctive nature of the chordamesodorm. In the adult vertebrate, tissue components of organs and organ systems can in general be sorted out readily as regards their derivation from the germ layers. Details and exceptions will be found in later chapters.

From the body ectoderm: the superficial portion (epidermis) of the skin and its extensions into the ends of the digestive tube (mouth, cloacal region); epithelial skin structures, such as hair and feathers.

From the neural ectoderm: the nervous system; the eye retina; certain other derivatives from the neural crest. From the mesoderm: connective and skeletal tissues; the musculature; the vascular system; most of the urinary and genital systems; the lining of the celomic cavities; the notochord.

From the endoderm: the gut lining and the substance of glands derived from

it (liver, pancreas); much of the breathing apparatus of gills or lungs.

It was once believed that the origin of various tissue types was absolutely restricted to one or another of the germ layers. In recent years, however, various exceptions have been discovered under both normal and experimental conditions, and there has been a tendency on the part of some to abandon the germ layer concept as meaningless. This, however, is a counsel of despair. In general we find that in normal development the embryonic cells and tissues do follow a consistent pattern of regional movement and arrangement of components. If nothing more, the germ layer terminology is useful as a description of the topography of development. It is, however, more than this. Experimental work has shown that, although in early stages there may be little differentiation between various regions of the embryonic germ layers, there is increasingly, in later stages, a limitation of capacities in different regions. The prospective faite in normal development of the germ layers and subsidiary areas of these layers is in general accord with the experimentally deduced story of their prospective potencies.

# 6

### THE SKIN

Forming a covering for the entire body, the skin, with its accessory structures, is an organ system performing varied and important functions. A tough "hide" is a protection against injury and attacks of predaceous enemies. The skin is a continous line of defense against the invasion of microorganisms and wards off injurious physical and chemical influences. Further, it may play a positive role in many ways— the regulation of body water and of salt content, the intake of oxygen, the elimination of wastes. As the part of the body in immediate contact with the outer world, the skin is the site of important sensory organs, and the nervous system, although withdrawn from the surface in the adult, arises, as we have seen, in continuity with the skin ectoderm.

The skin is not a single structural entity, but coasists of two parts, epidermis, and dermis, closely united but differing in nature and origin. The epidermis, ectodermal in origin, is superficial and essentially epithelial in nature; the deeplying dermis, of mesodermal origin, is primarily a fibrous structure. The epidermis is thin, the dermis thick; the epidermis gives rise to a host of different structures, is thin, the dermis thick; the epidermis gives rise to a host of different structures,

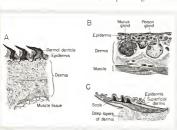
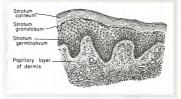


Fig. 75. Sections of the skin of A, a shark; B, a salamander; C, a teleost. (After Rabl.)

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Fig. 76. Section of the skin of the human shoulder, X 25. In addition to the germinative layer and stratum corneum, there is las here ji many areas of the skin in manmals an intermediate granular layer in the epidermis; in some situations there is further a transparent layer (stratum luciadum) between horny and granular levels. (After Maximow and Bloom.)



such as hair, feathers, various glands; the dermis is relatively simple and unitorm in composition.

Epidermis. In Amphioxus and hemichordates the epidermis consists of a single layer of columnar cells; in all true vertebrates it is a stratified epithelium. In fishes and water-dwelling amphibians (Fig. 75) it is a persistently simple structure, apart from the presence of glandular elements, and its entire thickness consists of "live" cells containing a normal protoplasm. There may, however, be present, here and in higher vertebrates, a dark pigment, melanin (derived by transfer from dermal pigment cells), and the superficial cells include a certain amount of keratin (a protein material abundant in cattle horn sheaths, fingernails and similar structures). These outer cells tend to be lost by wear or injury; they are constantly replaced from below, and are ultimately derived by the budding off of successive layers of cells from the basal layer of the epithelium. Superficial damage to the epithelium is readily repaired, but if through major injury, such as serious burns, a large area of this basal "mother" layer is destroyed, a recovering of the flesh by skin becomes difficult, if not impossible. The moist epidermis of many lower vertebrates is permeable to some degree and in most modern amphibians is a major breathing organ, richly supplied by blood vessels deeper in the skin.

With the assumption of a definitely terrestrial life by certain of the amphibians and by the amniotes, the nature of the epidermie is changed (Fig 76). Water loss, particularly, is a serious matter, and the surface of the skin becomes dry and impervious. The inner cells remain "live" structures, but as the surface is approached, the cells become flatter, lifeless and filled with keratin. The outer cell layers may be rubbed off and lost piecemeal (dandruff is an example) or shed seasonally in reptiles and amphibians. The transition between inner and outer portions may be gradual, as in land-dwelling amphibians, reptiles and birds. In mammals, however, there is a sharp contrast (Fig. 76) between a lower zone of live cells, the stratum germinativum, and the flattened dead cells of the stratum corneum on the surface.

Keratin Skin Structures. Throughout the higher vertebrates the keratinfilled epithelium develops into a variety of special structures. Simplest, perhaps, are thickenings or swellings of the stratum corneum, as, for example, in the "warts" of toads, or in the foot pads found on the under surfaces of the feet in many land-dwellers. In mammals (Fig. 77, A) such pads are characteristically 114



Fig. 77. Palm surface of the manus of A. an insectivore; and B. a monkey (macaque). The insectivore shows a presumably primitive critics ratio at the proximal end of the palm (III). III), palm be breen the base of successive digits (II' to II') and pads at the tip of each to (I' to I'). In ligher primates thee pads are replaced by patterns of friction ridges. (After Whipple).

present at or beside the base of each toe, with a pair in addition on the proximal part of palm or sole. In higher primates palm and sole are covered instead by a pattern of friction ridges (Fig. 77, B) which assist arboreal forms in obtaining a firm grip on the tree limb. In man, the great variation in the arrangement of the loops and whorks on the finger tips affords a ready means of identification.

In reptiles, thickening and hardening of the cornified epithelium results in the formation of horny scales or scattes (Fig. 78). In lizards and snakes there are generally overlapping scales, highly developed in snakes as an aid to locomotion. In crocodilians and turtles there are, in contrast, flat horny plates. It must be memphasized that these horny epidermal structures are not at all homologous with the bony dermal scales of fish; in many lizards, however, dermal bony scales underlie the superficial horny structures, and in turtles the horny plates form a superficial sheathing for the body armor.

In mammals and birds horny scales have for the most part disappeared; they persist, however, on the legs of birds, and on the legs and tails of a variety of mammals, notably rodents. The pangolin of the Old World tropics is notable as a mammal which has redeveloped a body covering of large horny scales.

Claws, nails and hoofs are keratinized epidermal structures tipping the digits of anniotes (Fig. 79), growing continually outward from a germinative layer beneath or at the base of the structure as the distal end wears off. Beneath the claw or nail tip is a layer of softer, less cornified material, the subunguis.



Fig. 78. Diagrammatic sections of reptile skin to show scale types. A. Lizard skin with simple, horny epidermal scales, gently overlapping. B. deeply overlapping horny scales of snake type; C. type of scale present in many lizards, with bony scale underlying horny element. (After Boas.)

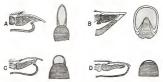


Fig. 79. Longitudinal sections and ventral views of terminal phalanges of mammals to show the build of claw, nail, and hoof. Toe phalanges, stippled; subunguis, fine stipple; epidermis of ventral surface of foot, hatched; epidermis of upper surface and horny material of claw, clear. A, Claw of carnivore type; B, a horne's hoof: C, a nail of a typical primate; D, a human nail. (After Boas.)

The claw. V-shaped in section and pointed at the tip, is the basal type; a nail is essentially a broadened modification. Hoofs are characteristically a development of ungulate mammals which walk on the tips of the digits.

Horns and hornlike structures are widespread in distribution, particularly among ungulate mammals. A true horn is seen in members of the cattle family, including sheep, goats and antelopes. The core of the horn is a spike of hone arising from the skull; sheathing this is an epidermal hollow cone of true horn substances. Neither core nor sheath is ever sheet. Although othen called a horn, the antier of the deer is quite a different structure. When mature it consists solely of hone; only during growth is it covered by skin in the form of "velvet"; no actual horn substance is present. As further points of contrast we may note that an antler is branched and is shed annually

Still other types of "horns" are found among mammals, and comparable structures are seen, although less commonly, in reptiles and even birds. We may note, for example, the simple, bony, hair-covered unshed horns of the giraffe; the American prongbuck's horn, with a branched horny sheath which is shed and a simple core which is not; the rhinoceros horn which is a fused mass of hairlike horny dermal papillae.

'Feathers. The possession of feathers is the distinguishing mark of the bird. Derived, it is believed, from reptilian scales, and primarily epidermal in origin, they perform two major functions in avian economy. As a body covering they are effective insulating devices, aiding in temperature regulation; bird flight is rendered possible by the development of large feathers forming the wing surface and the tail "rudder."

Three feather types may be distinguished (Fig. 80): the down feather, the filoplume and the contour feather. As the largest and most familiar (if most complicated) type, contour feathers may be first described. The mature feather is formed entirely from highly cornified epidermal cells. The base is the quill, a hollow cylinder with its eavity more or less filled by pith—the remains of mesodermal material present here during the development of the feather. At either end of the quill is an opening—an umbilicus. The quill lies in a folliefe, a cylindric pit extending down into the dermis but surrounded by an epidermal sheath.

Beyond the quill is the exposed and expanded portion of the feather, the vane. The axis is continued by the shaft or rachis, which (in contrast to the quill) is a

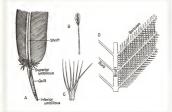


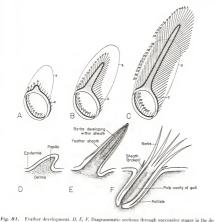
Fig. 80. Feathers. A. Proximal part of a contour feather; B. filoplume; C, down feather; D, diagram of part of a contour feather, to show interlocking arrangement of barbules. (After Gadow, Bütschli.)

solid structure. Outward from either side extend the major shaft branches, the barbs; cach harb is, in most birds, interlocked with its neighbors by tiny hook-bearing branches, the barbules. In nonflying ostrich-like birds, where smooth contours are unnecessary for wings or body streamlining, there is little development of barbule hooks, and the contour feathers may be fulfy plumes.

Basically similar but simpler in build are the down feathers which form the entire body covering of the chick and may, as an insulating layer, underlie the contour feathers over much of the adult body. As in contour feathers there is a quill, but distally there is no shaft, simply a splay of slender branches. Filophumes—"pinfeathers"—are still simpler, with a single hairlike shaft which, however, may terminate in a tiny tuff of barry.

In its initial stages embryonic feather development (Fig. 81) is comparable to that of a reptilian scale, for a cone-shaped epidermal papilla structure is formed, within which are mesodermal tissues. Beyond this point, however, feather development follows a course far different from that of a scale, for this papilla sinks inward, with formation of a follicle within which growth of the feather continues. In the formation of a down feather, the portion of the cone enclosed in the follicle becomes the quill, its epidermal covering becoming a comified eyilinder, the contained mesodermal tissues persist as a nutritive pulp until the feather matures. Distally, however, the outer layer of the epithelium separates as a sheath from a deeper layer which divides into a series of thickened longitudinal ridges. When growth is completed the sheath breaks down, and the ridges of epidermis beneath it are freed to become the spreading distal faliaments of the down feather.

More complicated, but basically similar, is the development of a contour feather. As in the case of the down feather a cone is formed, with its proximal portion remaining simple in nature as the future quill and with the epidermis of the distal portion separating into a superficial sheath and a deeper series of longitudinal ridges arising from a basal "collar" at the end of the quill region. The entire development of the complex vane structure takes place within the sheath (Fig. 81, A-d). One dominant ridge grows out from the collar as the future shaft; other ridge formed from the collar gradually migrate onto this shaft to form the barts; the barbules later form by outgrowth from the barbs. When the feather is fully formed THE SKIN 117



colours and the colours of the colou

within the sheath, this ruptures, and the feather has simply to unroll to attain its mature stage.

Feather replacement continues throughout life, with a basal segment of the papilla persisting at the bottom of the follicle as a feather matrix. Replacement may be a gradual, continuous process, but in many birds, particularly those of temperate and arctic regions, there is a seasonal phenomenon of moulting.

Hair. As an insulating device formed of keratinized epidermis, hair is a mammalian analogue to the avian feather. In other regards, the two structures differ greatly. There are differences in development, in contrast to feathers, there is no participation by the mesoderm in the development of hair beyond a basal apulla. Hairs, unlike feathers, are not modifications of horry scales, but are new



Fig. 82. Hair patterns of mammals to show presumed derivation from structures developed in the interstices between scales. A Part of the scaly tail of a tree shrew, with the hair (represented by dots) in this position; B, skin of a marmoset, with the hairs arranged in a similar pattern despite the absence of scales. (After De Meigires.)

structural elements of the skin. It is probable that hair evolved before our reptilian forebears had lost their scaly covering; in such mammals as retain scales, hairs are found growing in definite patterns between the scales; and even when (as usual) scales are absent, the same arrangement of hairs may persist (Fig. 82).

A typical hair includes the projecting shaft and the root sunk in a pit in the dermis termed the hair follicle. Both shaft and root consist (except at the very base) of essentially dead and heavily keratinized epidermal cells; around the root is a sheath which (as shown in Figure 83) may consist of several distinct layers of epidermis and dermis.

At the base, the root expands into a hollow bulb, enclosing a dermal papilla containing blood vessels and connective tissues. Surrounding the bulb is a bala layer of "live" cells of epidermal origin, the hair matrix, from which are budded off the cells which form the hair root and shaft. Adjacent to the follicle and emptying its oily lubricating material into it may be found a sebaceous gland (cf. p. 120); each hair is further provided with a small muscle which by contraction may erect the hair (and by its pull on the skin cause "gooseflesh").

In the embryonic development of hair (Fig. 84) there is no projecting mesoderm-filled papilla, as in the case of a feather; instead there is a downward growth

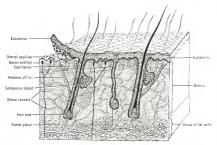


Fig. 83. Section of mammalian skin, to show particularly hair, glands and accessory structures.

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Fig. 84. Hair follicles from a 3-months human embryo, showing successive stages of development at A, B, and C. (From Arey.)

of a solid column of epidermal cells. At the base of the column there form a hair matrix and an enclosed mesodermal papilla; the column of epithelial cells above is hollowed out to form the hair shaft. No more than a feather is a hair a permanent structure; most hairs are cast off and replaced throughout life, either as a gradual process or as a seasonal shedding of the coat. Resorption takes place at the bulb; a new hair begins its development from the matrix cells.

All hairs contain pigment to some degree. Melaniu, derived from dermal pigment cells, is the common substance, producing in various concentrations shades of brown and black. A related pigment is responsible for reddish tinges; air bubbles present in the hair may lighten intensity of the color and when abundant may, with pigment reduction, produce gray or white hair.

Mammalian hair is highly variable in numerous regards—in thickness, length, and coarseness, in distribution over body regions, in arrangement of hair tracts, in the slant of hairs in various regions, and so forth. Hairs rounded in section tends to be straight, and if stoutly developed may become sensory ribrissae (as in the cat's "whiskers") or protective bristles or spines; hairs oval or flattened in section are more readily bent and may result in a curly or woolly covering.

Skin Glands. Clandular structures develop in the epidermis of every vertebrate class. In fishes and amphibians mucus-producing cells are generally present and widely distributed and in amphibians they take the form of alveolar mucus glands. In relatively rare instances poison glands, usually associated with spiny structures, are found in fishes. In many amphibians there are glands producing poisons of a variable degree of toxicity; these are termed granular glands because of the granulation of the protoplasm of the secreting cells.

An unusual development in deep sea fishes is that of luminous organs, photophores (Fig. 85), which may frighten enemies, lure food or afford recognition at mating time. These structures appear to be modified mucus glands; accessory organs which may develop include a pigment-backed reflector and a lens, giving much the build of an automobile headlight. Light production may be due either to

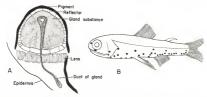


Fig. 85. A, Section through a light organ of a teleost (Cyclothone). Part of the duct leading in from the body surface is seen. B. Light organs of a small teleost (Myctophum). The organs are in black. (After Brauer).

phosphorescent bacteria or to complicated processes of oxidation in the glandular cells.

In the hard dry skin of reptiles, glands are little developed, and the same is true of birds, except for the usual presence of an oil-secreting preen gland above the root of the tail. In mammals, however, several new types of glands make their appearance. Oily sebaceous glands are associated with hair follicles (Fig. 83) but may persist in regions where hair is absent. Sureal glands (Fig. 83) produce a way secretion containing salts, urea and other waste products. Through evaporation of their product on the skin they are effective in ading temperature regulation.

A further mammalian gland type—one to which, in fact, the class owes its name—is that of the milk-producing mammary glands. Thought to be modified sweat glands, they are well developed in the female of every group. In monotremes

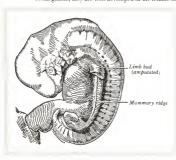


Fig. 86. Mammalian embryo, to show mammary ridge or "milk line." (From Arey.)

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there are simply two bundles of discrete glands which discharge their secretion into a depression on the belly surface; in other groups the gland openings are concentrated in projecting teats or nipples. The embryonic development of these glands usually begins as a pair of longitudinal swellings, the mammary ridges (Fig. 86) running ventrally the length of the trunk; a variable number of concentrations of tissue may occur at a variety of points. The number of teats is generally related to the number of young usually borne. When few in number, they may be either abdominal in position, as in many ungulates, or in the pectoral region, as in higher primates; in such forms as pigs and many carnivores, where litters are large, two long rows of nipples may be present. An active milk gland typically contains clusters of alveoli, from which duets lead toward the surface. Properly, the term nipple is applied to types in which the ducts lead directly to the tip; in a teat (as in the cow) the ducts empty into a storage reservoir, whence a large duct leads to the surface.

Dermis. Thicker but less varied in structure than the epidermis is the dermis or corium (Fig. 83). This basically consists in most groups of a dense connective tissue—the material which, after appropriate treatment, may become commercial leather. The deep portion of the dermis is generally looser in texture, and, further, is often a major locus for the development of fatty tissues. Fat is an excellent insulating material; in whales, as the thick "blubber," it substitutes for the absent hair in this regard.

In mammals, especially, striated muscle tissues, derived from underlying body muscles, may attach to the under surface of the skin. The sensitivity of the skin is due to the presence in the dermis (seldom the epidermis) of nerve fibers; some end freely, others—most notably in mammals—terminate in sensory corpuscles. Girculatory vesses her abundant, in the form of capillary networks and of lymphatics. In forms with a moist skin this rich vascular supply permits the exchange of materials with the surrounding medium, and the skin acts as a major breathing organ in many amphibians and some bony fishes.

The thick connective tissue of the dermis constitutes a major defense against injury. In most bony fishes, however, this layer is in great measure replaced by stouter defenses in the form of bony scales or plates, these are parts of the dermal skeleton and as such are described in the chapter following. Except for the skull and shoulder region this dermal armor is much reduced or absent in most land vertebrates (turtles are a conspicuous exception) and it is likewise absent in cyclostomes and in sharks, except for the small denticles embedded in the skin of the latter.

Offhand, one would assume that the more common fibrous condition of the dermis in modern vertebrates is primitive and that the presence of bone in the dermis is secondary. As we have seen, however, the story of vertebrate evolution strongly suggests that the reverse was the case. The oldest known vertebrates were armored, and it is highly probable that the absence of dermal armor in living jawless forms and in sharks is due to degeneration.

Chromatophores. Skin color in vertebrates below the level of mammals or birds is due in great measure to special color-bearing cells, the chromatophores, located in the outer part of the dermis (Fig. 67). These are typically stellate in form and contain numerous granules. Common types include (1) melanophores, with a dark brownish pigment, 2d lipophores, which of vyellow pigments, and (3) guanophores, which contain not pigment but tiny crystals which by light reflection may alter the effect of the pigment materials. Nearly all the varied colorations of fishes,

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Fig. 87. Enlarged surface view of a piece of the skin of a flounder, seen by transmitted light, to show the three types of chromatophores present—pigmented melanophores, lapophores, and crystalline guanophores (or iridocytes). (After Norman.)

amphibians and reptiles are due to chromatophores of these three types, present in varied numbers and varied arrangements. In many instances striking color changes may occur—the chameleon is proverbial in this regard and flounders are equally in the variety of color and color patterns which they are able to display. In part these changes are related to shifts in the position of chromatophores of the three types, but in the main they are due to changes in the distribution of the color gamules within the individual cell. If the granules are dispersed, the effect is maximum; if concentrated in a tight cluster, little color appears. Color changes may result from direct stimulus of light or heat but are more commonly a response to the color scheme of the environment, based on information reaching the brain through the eyes and transmitted to the chromatophores either by hormones (mainly from the pituitary), by nerves of the autonomic system, or (as in teleosts) by a combination of the two methods.

Although the chromatophores are situated in the dermis, the embryologic story shows that in many cases—perhaps in all—these cells are not part of the mesodermal tissues. They rise in the embryo from the neural crest and migrate thence to their ultimate peripheral positions.

Temperature Regulation. Proper functioning of the vertebrate body can take place only over a restricted temperature range. In lower vertebrates the internal temperature tends to follow that of the environment, and little regulation is possible; but in mammals and birds body temperatures are regulated, under the control of a neural "thermostat" in the hypothalamic region of the brain, so that the internal temperature varies little from a norm which is generally within a few degrees of 100° F. Most heat loss takes place through the skin, which is thus of the greatest importance in regulation. The connective tissue of the dermis and, most especially, its fatty tissues, are insulating in nature, as are bair and feathers as well. In addition, the skin can act in a positive way in temperature regulation. Hair and feathers are adjustable regulators, and evaporation from sweat glands produces a cooling effect. Highly important is the vascular system of the skin, which is under control of the autonomic nervous system; with distended arterioles and capillaries in a "lushed" skin heat is lost rapidly; with constriction of the arterioles (and a blanched skin), heat is conserved.

# 7

### SUPPORTING TISSUES—THE SKELETON

Most of the functionally "active" tissues of the body are epithelia or tissues derived from epithelia. But were the vertebrate body to be composed solely of such tissues, it would be a flabby and amorphous mass. Materials are needed to back up and reinforce the epithelia and their derivatives, to weld them together into a formed body, to protect this body, and—particularly in non-aquatic forms—to give it strength and support. Such materials are described in the present chapter. The notochord is a distinctive structure of this sort. Connective tissues are widespread and important. Most prominent in vertebrates are the cartilages and homes that compose the skeleton.

### NOTOCHORD

The notechord is an ancient structure, present even in such lower chordates as Amphioxus and larval tunicates. As has been seen, it arises embryologically from the median portion of the mesodermal tissues, extending in embryonic vertebrates from a point beneath the brain backward along the length of trunk and tail. Its cells are soft and gelatinous; the notochord is, however, surrounded by a sheath and membranes which render it a relatively strong yet flexible structure.

A well-developed notechord persists in the adult in many lower vertebrates notably evclostomes, in which the backbone is little developed (Figs. 17, 106, pp. 37, 140). In most fishes and in tetrapods, however, it is progressively replaced by the central elements of the vertebrae, which develop around it and give greater strength if less flexibility. As vertebrae become more highly developed, the notochord is reduced in importance. It is always prominent in the embryo, but in most instances it is soon restricted, during development, by the vertebrae. In many fishes and more primitive tetrapods it may expand between successive vertebral centra but constrict within each segment, so that its contours resemble those of a series of hour glasses set end to end. In most vertebrates it is further reduced, so that in the adult it is represented only by gelatinous materials which may persist between successive centra of the vertebral column.

### CONNECTIVE TISSUES

Even in such lowly invertebrates as the coelenterates, which lack a true mesoderm, there is generally interposed between inner and outer layers an intermediate



Fig. 88. Loose (areolar) connective tissues. (After Millard, King and Showers, Human Anatomy and Physiology.)

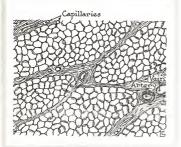


Fig. 89. Fatty (adipose) tissue under low magnification. Lobules of fat cells are separated from one another by partitions of fibrous connective tissue. (From Millard, King and Showers, Human Anatomy and Physiology.)

zone of more or less gelatinous material, sometimes fibrous, and containing sparsely distributed cells; such material aids in filling out the form of the body and is comparable to the mesenchyme of the vertebrate embryo. In the adult vertebrate the most direct products of the embryonic mesenchyme are the connective tissues which form the "stuffing" of the body and reinforce the epithelia of many of the body organs. In simple form this tissue (Fig. 88) is of a loose type, with a gelatinous ground substance containing a network of small branching reticular fibers and, more prominently, long and slender collagenous fibers, flexible but inelastic, which are formed by the spindle-shaped or stellate connective tissue cells (fibroblasts). In other cases, such as the dermis of the skin (Fig. 83) the connective tissue is compact, with dense masses of fibers which form a feltlike structure. Most connective tissues contain a small percentage of coarse yellow elastic fibers, and in a few instances this fiber type is dominant. Tendons, forming the attachment of many muscles, consist of bundles of connective tissue fibers; ligaments are comparable structures uniting skeletal elements\*; fasciae are sheets of connective tissue investing muscles or other objects. Fatty or adipose tissue (Fig. 89) is a connective tissue modified for fat storage, commonly developed beneath the skin or in mesenteric folds among the abdominal organs.

### SKELETAL TISSUES

From a physiologic or biochemical point of view the skeleton is sometimes thought of as a relatively inert organ system. From a broad functional viewpoint, however, it is of the greatest importance. Evolved in phylogeny from the connective tissues and developed in ontogeny from them, or from the mesenchyme which precedes them in the embryo, the hard skeletal structures are vital in welding together and protecting the softer organs and helping in support and in maintenance of body form. Almost all the striated musculature attaches to the skeleton, which is hence the agent through which bodily movement is accomplished.

Cartilage. Two skeletal tissues are characteristic of vertebrates—cartilage and bone. Although both are specialized derivatives of the connective tissues and arise from mesenchyme, they differ markedly in nature and in mode of origin.

Typical hyaline cartilage (Fig. 90) is a flexible material with a translucent, glassilite appearance. Is firm ground substance, or matrix, is mainly a polysaccharide, forming a firm gel through which is spread a network of connective tissue libers. Throughout are spaces containing cartilage cells, which are generally rounded and without the branching processes characteristic of bone cells. In most cartilages blood vessels are absent, and hence the nutriment received by these cells must reach them by diffusing through the ground substance. The outer surface of a cartilage is covered by a layer of dense, cell-containing connective tissue, the peri-chondrium.

There are numerous variants from this ordinary type of cartilage. In sharks, particularly, there is frequently present calcified cartilage, which simulates bone in that a deposit of calcium salts is laid down in the cartilage matrix. Elastic cartilage, seen, for example, in the mammalian ear pinna, gains flexibility through the presence of many elastic fibers in the ground substance. Fibrocartilage, frequent in the region of joints and of muscle and tendon attachments, is transitional in composition between dense councetive tissues and cartilage.

<sup>\*</sup>Certain mesenteries, attached to viscera, are also termed ligaments.



Fig. 90. Section through part of a cartilage (from the sternum of a rat). The surface layers (at the top) show a fibrous condition transitional to the perichondrium. (After Maximow.)

In cartilage formation, mesenchyme cells round up and develop between themselves the characteristic cartilage ground substance and fibers. Frequent cell divisions are seen in a growing cartilage; we may find as a result cells in pairs or quartets, the members of which gradually separate as more matrix is deposited between them. Cartilage, like bone, may grow by the addition of new cells to its our surface; but in contrast with bone, it can also grow by internal expansion—a swelling of the ground substance.

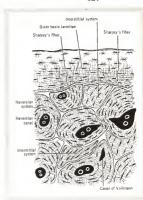
Cartilage is essentially a deep, internal skeletal material, rarely present on or near the surface of the body. It is always abundant in the embryo and young. In higher living vertebrates and in many of the older fossil types of lower vertebrates the adult skeleton is mainly formed of bone, and cartilage is reduced. Only in living lower vertebrates—cyclostomes, Chondrichthyes and a few degenerate Osteichthyes—is cartilage a major skeletal material in the adult.

Cartilage is generally a deep tissue, an embryonic tissue, a relatively soft and pliable and readily expandable tissue.

Bone (Fig. 91). Bone is the dominant skeletal material in the adult of most vertebrate groups. Like cartilage it consists of transformed mesen-chyme cells enclosed in a ground substance containing connective tissue fibers. Beyond this, however, the two materials differ markedly. The bone matrix rapidly becomes a hard, opaque material containing phosphate and carbonate salts of calcium. The bone cells (and the spaces—lacunae—in which they are enclosed) are irregular, star shaped; their branching processes continue in tiny canals—canaliculi—10 reach neighboring cells. In contrast with cartilages, bones are penetrated by blood vessels, but since the solid matrix is impervious to nutritive materials, the cells receive sustenance by way of the system of canaliculi. Unlike cartilage, bone cannot evpand: it can grow only by the addition of new external layers formed from the dense connective tissue, the periosteum, which surrounds it.

Bones have a complex microscopic structure. Many areas—particularly surface regions—consist of compact hone. But in the interior of bones there is often found a spongy type, in which the bone material is reduced to a lattice-like framework, vascular or falty tissues forming a bone marrow in the interstices. Much of the substance of any bone is haid down embryologically in the form of successive layers.

Fig. 91. Bone structure. A ground this section through a manualism neteractural. Toward the top through a manualism neteractural. Toward the top (outer) margin are parallel lamellase of bone formed from the periotenum within are a number of haversian systems cut at various angles. The "interestitial systems" includes remains of earlier formed bone layers not destroyed when the present haversian systems were created. A cementing substance binade the different bone areas together, "Volkmann's canals" carry blood vessels from the surface or bone marrow early to haversian systems. Sharpe's fibers are connective those when the control of the surface of the control of the surface of the surface of the control of the surface of the surface of the surface of the those substance. (Mer Maximos and Bloom.)



or lamedlae, but throughout life there continues a process of reworking of bony materials, by absorption of old bone and the redeposition of new. Common is bone destruction by the "eating out" of tubular channels in the bone substance, the destruction being due to bone-destroying cells termed osteodasts. In these channels bone is redeposited in concentric layers, leaving a small central canal containing blood vessels and nerves; the whole structure formed by this process of redeposition is a haversian system.

Bane Development. Two radically different modes of bone formation—i.e., ossification—are to be seen in the embryo. The simpler is the formation of membrane bone (Fig. 92), in which the bone forms directly from mesenchyme. A group of bone-forming cells—osteoblasts—lay down between them a thin, irregular plate or membrane of dense matrix in which bone salts are rapidly deposited. This plate gradually expands at its margins and thickens on either surface by the deposition of turther layers, the enclosed cells becoming the definitive bone cells, or osteocytes. In fishes other than cyclostomes and sharklike forms, membrane bones, or dermad bones, usually form over nearly the entire surface of the body (including the mouth cavity), taking the form of large plates anteriorly and of bony scales over the trunk and tail. In higher vertebrates, in the usual absence of bony scales or body armor, the extent of dermal bone formation tends to be restricted to the head and shoulder region.

Quite different and more complicated is the formation of endochondral bone (Figs. 93, 94). This is primarily the replacement of an embryonic cartilage by bone;

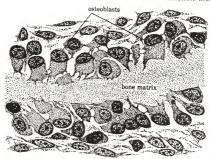


Fig. 92. Section through a dermal bone of the skull at an early stage of development. A thin sheet of bone matrix has already formed, surrounded by bone forming cells—osteoblasts—some of which will presently be enclosed, as osteocytes, in the growing bone. (From Windle, Textbook of Histology, McGraw-Hill Book Company.)

but, as will be seen, a good fraction of the process even here consists of laying down bone directly in membranous fashion external to the cartilage.

In such typical internal structures as long limb bones of tetrapods a cartilage tends to assume the shape of the adult bone at an early stage and tiny size. Presently modification and degeneration of the cartilage begin near the middle of its length. The cartilage cells swell and arrange themselves in columns, and the matrix between them calcifies. Blood vessels break in from the surface; the cartilage of this area is destroyed and bone is laid down in its place. From this central area the process of replacement continues toward each end of the element to form the shaft of the bone—the diaphysis:

If the embryonic cartilage failed to grow, it would be completely replaced by bone in short order. But lengthwise growth of the cartilage, mainly by internal expansion, does continue and proceeds at about the same pace as the ossification within it. The cartilage, so to speak, leads the bone tissue a long "stern chase" which is not concluded until adult size has been attained. With complete ossification, growth stops, for internal skeletal elements are usually articulated at the ends with their neighbors and bone cannot be readily added on the articular surfaces.

In lower vertebrates, generally, internal bones ossify from a single center, and their ends are often largely cartilaginous even in the adult. But in mammals (and to a very limited extent in reptiles) accessory ossifications—epiphyses—are found (Fig. 94). These are characteristically developed at the ends of long bones or on prominent processes for muscle attachment. These accessory centers may produce ossification (and hence strengthening) of the articular region of the bone long before

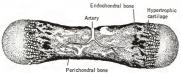


Fig. 93. Section of a mammalian embryonic metapodial, in which ossification is taking place in the shaft (hone in black). Perichondral ossification is taking place superficially. At either end is normal cartilage; toward the center of the shaft the cartilage becomes "hypertrophic"; the cells are swollen and arranged in rows; calcification occurs, followed by their replacement with dermal hour

shaft growth is completed. Between epiphysis and shaft there is long a persistent band of cartilage. This band would at first sight seem to be a relatively inert and functionless region. Actually, of course, it is highly important. This is the one zone of growth; the cartilage here is continually growing and is as constantly replaced by bone from shaft and epiphysis. Once this band is eliminated, shaft and epiphysis unite; growth is ended.

Although much of the development of an internal "cartilage bone" takes place by the replacement of cartilage, this is not, as one will readily see upon reflection, the whole story. The original cartilage had but a very small diameter; as grown occurs, the cartilage at the two ends becomes much broader, but if the entire shaft consisted entirely of replaced cartilage, the adult structure would be shaped like an hour glass, with a very thin middle portion. This imperfection is rectified by the direct formation around the shaft of layers of perichondral bone, formed much in the fashion of membrane bone, thus giving the necessary adult thickness.

The process of endochondral bone formation in higher vertebrates was long thought to be an example of ontogenetic recapitulation of phylogenetic history. It was assumed that the cartilaginous condition of the skeleton seen in cyclostomes

Fig. 94. Ossification and growth in a long bone of a mammal. Λ cartiligenous stage, B, C, Deposit of spongy, endochondral bone (stippled) and compact, perchandral lone (blick), B, Appertance of an epiphysis at either end. E, Aperican constitution of the control of the conwing to recorption of endochondral bone. The growth of the bone is confined to the thin strips of actively growing cartilage between shaft and epiphyses. F, Union of epiphysis with shaft, leaving articular cartillages on end saffaces; enlargetion of the compact of the compact of the control of the control



and sharks was a primitive one, to which the cartilaginous state of the skeleton in the embryo of higher forms was a true parallel. However, present evidence, reviewed in Chapter 3, suggests that this is not the case, but that the primitive vertebrates had well ossified skeletons as adults and that no recapitulation is involved.

If so, why this roundabout way of forming bones? Why cartilage at all, if it is not an "ancestral reminiscence"? The answer may be deduced from the fact that it is only deeplying bones that are preformed in cartilage. Dermal elements, usually platelike in nature and usually lacking any major muscular attachments or complex plate in the remaining of the surfaces and margins. But internal elements of the limbs, backbone and braincase rea usually attached in complex fashion to other skletal structures and, particularly toward the ends of limb bones, may have complex relations with muscles, blood vessels and nerves. They cannot grow by plastering new layers of bone to their surfaces; and they could not, if formed of bone, expand. What is needed for growth of such structures is some sort of pliable material which can grow without disturbance of surface relations. Cartilage, capable of growth by internal expansion, is an ideal embryonic adaptation for this purpose. Except where degeneration has occurred—in various fishes and amphibians—bone is the normal adult skeletal material in a vertebrate, cartilage is indisenseable embryonic auxiliary.

Joints. Bones and cartilages are joined to one another by structures of varied types. In such cases as bones of the skull where movement is not necessary or desirable, two elements may be firmly connected with one another; lines of separation between two such elements—sutures—may remain visible, or the two may fuse in the adult. Such an essentially immovable type of union is a synarthrosis. A freely movable joint is a diarthrosis (Fig. 95); a well-formed, liquid-filled joint cavity is frequently developed.

Classification of Skeletal Elements. The skeleton includes a wide variety of elements of varied form, structure, function, position and embryonic origin, associated in variable combinations. Classification of them is difficult; although no method is absolutely satisfactory, we here adopt the following scheme of major subdivision:

Dermal skeleton		Axial
Endoskeleton	Somatic Visceral	Appendicula

We have noted above the marked embryologic distinction between bones formed in membranes in the dermal layers of the skin and the deeper lying endo-chondral elements. Among the latter a distinction may be made between two groups of unequal size. The visceral skeleton includes the cartilages or bones associated with the gills and skeletal elements (such as the jaw cartilages) derived from them. These, as will be seen, have in general an embryonic origin quite different from most of the remainder of the internal skeleton, here termed the somatic skeleton. This last major division includes in all vertebrates the vertebrae, ribs (when present) and, anteriorly, the braincase. These structures are the axial skeleton. Paired limbs are present in most forms and are prominent in tetrapods; the structures of the limbs and limb girdles belong to the somatic group but may be distinguished as the appendicular skeleton.





In certain instances we find that structural units of the adult skeleton contain elements derived from two or more categories. Thus, for example, the shoulder girdle frequently contains both dermal and endoskeletal components; the lower jaw in many forms includes visceral and dermal elements. Most complex of all is the skull, which in bony fishes and land vertebrates includes dermal, axial and visceral structures in its formation.

### DERMAL SKELETON

Fishes. The skin over most of the body of many living vertebrates contains no hard skeletal parts; but dermal bony structures are usually present in the head region, at least, and the fossil evidence leads to the conclusion that ancestral vertebrates were ensheathed in armor, composed in the main of dermal bone. Such armor completely encased the most ancient jawless ostracoderms, covered part or all of the body of the most primitive jawed fishes, the placoderms, and is preserved in most members of the great fish group of Osteichthyes. Armor is absent in cyclostomes and is found only as skin dentiteles in the sharklike fishes; this condition, once thought to be primitive, now seems quite surely to be a degenerate one.

In ancient ostracoderms and many placoderms there was present a pattern of microscopic structure in excless and plates which, with variations, persisted into the primitive bony fish stage (Fig. 96, A). A middle layer consisted of spongy bone, presumably containing blood vessels; inner and outer layers were compact. The outer surface was frequently ornamented by tubercles or ridges. The substance of these surface structures was formed of a material much like the dentine of a tooth (cf. p. 233), with a "pulp" cavity beneath and with a surface layer of hard shiny material comparable to tooth enamel. The whole tubercle, in fact, was toothlike, and it is highly probable that teeth are actually derived from such structures.

Among early bony fishes two types of plate and scale structures were present. In the primitive sarcopterygians was the cosmoid scale (Fig. 96, B), so named

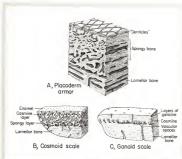


Fig. 96. The structure of dermal plates and scales in primitive vertebrates. 4. Devonian placoderm. B, Primitive crossopterygian with a cosmoid scale. C, A Paleozoic ray-finned fish with a ganoid scale. (After Kiser, Goodrich.)

because the substance of the tubercle consisted of cosmine, dentine-like but with branching rather than simple tubules running into it from the pulp cavity. Such scales were present in typical crossopterygians and the earliest lungfish, but the structure became simplified in later members of both groups, and the modern lungfish scale consists simply of a rather fibrous and leathery type of degenerate bone.

In primitive ray-finned fishes there was present, in contrast, the true ganoid scale (Fig. 96, C), differing from the cosmoid type in that during growth there was laid down on the outer surface layer after layer of shiny enamel-like mater-irac was laid down on the outer surface layer after layer of shiny enamel-like materials in the surface. Today only the African Polypterus and the gar pikes retain the ganoid type, and in modern teleosis the scales (much as in the parallel case of the lungfishes) are reduced to simple this structures of plable bonelike material.

Although we are confident that the eyelostomes are descended from armored ancestors, their skin is absolutely devoid of armor. In the Chondrichthyes there are sometimes fin-spines of a dentine-like nature, but the skin is otherwise bare except for the isolated demad denticles or placoid "scales" (Figs. 75, 4, p. 112, 97; 216, p. 283). These resemble teeth in structure, with a pulp cavity, a tooth substance of dentine and a shiny enamel-like surface. It was once believed that dermal plates and true scales resulted from a fusion of such denticles. It now seems more probable that the reverse is the case; that the dermal denticles are the last, superficial remains of ancestral armor, the deeper layers of which have, so to speak, melted away.

In fishes with skin armor the anterior part of the body is covered not with discrete scales but with large bony plates over the head, gill and shoulder region. In the ancient ostracoderms and placoderms these plates are arranged in varied patterns which are difficult to compare with those of modern forms. In bony

Fig. 97. Shark dermal denticles. A, Section through a denticle; B, Side and surface views of denticle. Abbreviations: D, dentine; D', dermis; E, hard, enamel-like surface of denticle—vitrodentine; E', epidermis; PC, pulp cavity. (From Dean.)



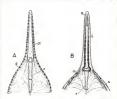
fishes the general pattern is of a more familiar type, although certain of the individual bones are highly variable. There is a well-defined cranial shield which forms part of a typical skull; bony plates are associated with the lower jaw and the inner surface of the mouth; there is, further, a dermal shoulder girdle. These will be discussed later. There may be noted the presence of a series of opercular elements covering the gill region (Figs. 32, 108, 154, 157; pp. 52, 141, 181, 183).

We may parenthetically discuss here the nature of the rays which stiffen the peripheral portions of fish fins, both median and paired (Fig. 98). Primitively, it would seem, the fins were covered with scales similar to those on the rest of the body. In higher bony fishes these tend to be modified into clongate bony rays, the lepidotricha. In addition, the fin tips in hony fishes may be additionally stiffened by tiny horny rays—actinatrichia—and in sharks larger rays of this sort—termed ceratorichia—are the sole supports of the fin web.

Tetrapods. Of the originally complete dermal covering of their ancestors, tetrapods have retained dermal elements in the skull, jaws and usually the shoulder girdle. The remainder of the dermal covering tends to be lost. In modern amphibians there is no dermal covering of the trunk and tail save for vestigial scales in the Apoda. In early amphibians and reptiles remains of scales persisted on the belly, and these are retained as V-shaped jointed rods, the gastralia, in Sphenodon, lizards and crocodilians. In birds and mammals even these last vestiges of the original armor have vanished.

The skin, however, retains its potentialities of forming dermal bone, and in many reptiles and a few mammals there has been a redevelopment of armor struc-

Fig. 98. Sections through the dorsal fin of  $A_s$  a shark;  $B_s$  a ray-finned fish; to show the nature of the fin supports.  $a_s$  Actinotrichia;  $c_s$  ceratoririchia;  $d_s$  dermal dentiele;  $l_s$  lepidotrichia;  $m_s$  muscle tissue at fin base;  $r_s$  skeletal supports of fin;  $s_s$  bony scales, (From Goodrich.)



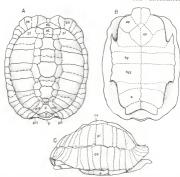


Fig. 99. A, Dorsal, R, ventral and C, lateral vices of the shell of a tortoise (Testado). Sutures between bony plates in solid line, outlines of homy scutes in broken line. Abbreviations: en. entoplastron; ep. epiplastrom, hy, hyoplastron: hyp. hypoplastron: an, mench; at 1-ar, nearlis; p. p. p. plates (post-neurals); pe, peripheral plates; p. l., most posterior (eleventh) peripheral; pl., pleural plates; x. xiphi-plastron.

ture. In lizards there are frequently bony scales underlying the horny scales of the epidermis; in crocodilians there may be a partial armor of subquadrate bony plates, and certain dinosaurs and other extinct reptiles were armored. Among mammat the armadillos have developed a bony carapace; their extinct cousins, the glyptodouts, had a comparable bony covering developed to a high degree.

Turtle Armor (Fig. 99). The most highly developed armor of any land vertebrate, living or extinct, is that of the Chelonia. Beneath the horny scutes that cover the body of most turtles there is dorsally a rounded, arched compace of bone and ventrally a flattened plastron; the two parts of the shell are connected at the sides by a bridge of bone, while front and back of the shell are open for the head, limbs and tail. Notable in the carapace is a median series of neural elements above the backbone, with costals, supported by rish, on either side, and a row of marginals around the margins. In the plastron there are typically four pairs of plates and an unpaired median element. The three plates at the anterior end of the plastron are modified dermal bones of the shoulder girdle; all the remaining elements of carapace and plastron are new developments.

## AXIAL SKELETON

Amniote Vertebrae. The host of skeletal structures remaining for description are endoskeletal, lying (in contrast to the dermal elements) deep within the

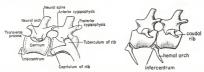


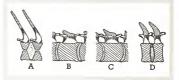
Fig. 100. Left, two trunk vertebrae of an early generalized reptile (anterior end to the left). Right, two caudal vertebrae.

body and first formed in the embryo in cartilage. Most of these internal structures belong to the system here termed somatic; they are formed (in contrast to those of the visceral system) from mesenchyme of mesodermal origin. Apart from the special category of limb supports, the somatic skeletal elements can be classed as axial.

The major axial structure is the vertebral column, which in most vertebrates replaces the notochord in the adult as the main longitudinal girder of the body and extends upward in each segment to enclose and protect the spinal cord. We may first consider the relatively simple and uniform structure of the vertebrae which compose the column in amniotes (Fig. 100) before considering the wild assortment of variants seen in lower vertebrate classes. A major element is the centrum, essentially a spool-shaped structure functionally replacing the notochord. Primitively the notochord persisted in the adult amniote in much reduced form, piercing the center of the centrum, but usually this ancient structure has vanished. The centra were hollowed at each end in early reptiles-the amphicelous condition (Fig. 101, A)—and this condition persists in some reptiles. Usually, however, the centra are more highly developed and their ends are apposed to those of their neighbors (Fig. 101, B-D). If the centra are flat-ended, the condition is termed acelous; if concave in front, convex behind, procelous; if the reverse of this last, opisthocelous. In some reptiles there are present in the trunk small intercentra wedged ventrally between successive centra. In reptiles and mammals generally these persist in the tail; here they bear hemal arches, consisting of a pair of rods extending ventrally to enclose the caudal blood vessels and meeting below in a spine separating the tail muscles of the two sides.

Above the centrum on either side rises a neural arch, sheathing the nerve cord; gaps between successive arches allow space for the exit of the spinal nerves. Above,

Fig. 101. Longitudinal sections through amoite vertebrase of various types (anterior end to the left). A Primitive amphiculous type; the form represented is pierced through the centrum by an opening for a continuous notochord. B. The opisithocelous type. C. The proceedous type, D. Essentially an acelous type, but with centra slightly bisconave and with room for an intervertebral disc. (After Gregory.)



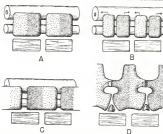


Fig. 102. Diagrams to illustrate the manner of utilization of monochyme in the formation of amoince vertebrae. As is diagrammatic vertical action of the selections of two somities, nerve cord and non-chord are shown behind them, and below is arbitrarily figured a portion of the musculature belongage to these somities. Be it selections have up in into an entire and posterior balves, which more associated. There have d with the adjacent halves of neighboring selectionses. These newly formed selections are directly and in D is diagramment of the contract of the selection of the desired properties of the desired

the arches meet to form a neural spine. At either side there is often a prominent transverse process for the attachment of a rib tubercle. In tetrapods—and in a few fishes—each pair of arches articulates with its neighbors fore and aft by "yoking" processes, the zygapophyses. The anterior zygapophyses terminate in surfaces facing inward and upward, which meet corresponding processes facing downward and outward on the opposed posterior zygapophyses of the preceding vertebra (for mnemonic purposes one may recall that in any procession, those at the front of the parade are up and in—those at the rear, down and out).

In the discussion of mesoderm differentiation we have noted that there was a proliferation of mesenchyme from the medial side of each somite—the area known as the sclerotome (Fig. 68, p. 105). It is from this material that the vertebrae are formed. One might assume that each vertebra would form from a single sclerotome, since there is a correspondence in numbers. Actually this is not the case—in ammiotes, at any rate. Each sclerotome divides into two parts, and each vertebra is formed from a fusion of adjacent halves of two successive selerotomes (Fig. 102). On reflection it is seen that this apparently odd development is a logical and functionally necessary one. The muscles of the trunk attach to successive vertebrae and ribs. The trunk muscles are primitively segmental in arrangement, and hence it is necessary that the skeletal elements to which they attach be alternated with them. This condition is brought about by the recombination of myotome halves, which places the vertebrae, and the ribs developed from them, in a proper intersegmental position.

Anamniote Vertebrae (Figs. 103, 104). The history of the neural

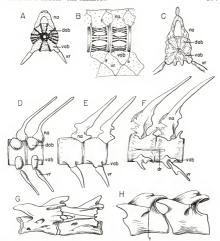


Fig. 103. A.-F. Fish trusk vertebrar. A. Coss-section of a vertebra of the shark Lamus, showing and bases wedged into centrum. The dark areas are calcified. B. Lateral view of the segments of the column of the same shark. Elements between the neural arches complete a closed take for the spiral cords; a complex of small elements represents bort ventral risk [e. hemal arches). The dorsal arch base covered by the base of the neural arches. C. A cross-section of a vertebra of a young Amis; both dorsal and vertal arch bases are visible and distinct from the centrum proper. E. Adult vertebras of the same than the case of the neural arches. The contract of the same than the case are conceiled by the neural arches. As the same than the contract of th

arches in lower vertebrate groups is fairly straightforward. Typical arches are present in most fishes and in amphibians, but in sharks additional elements are formed between the neural arches and in lampreys two pairs of small arches are present in each segment; in hagishes neural arches are absent allogether.

The history of the centrum is a more complex matter (Fig. 105). Cyclostomes have no centra whatever—merely a large, unconstricted notochord—and hence can be considered vertebrates only by courtesy. In sharks (Fig. 103, A. B)

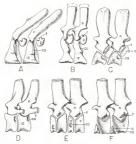


Fig. 104. The evolution of vertebral structures from crossopterygians to primitive tetrapods and reputes. A flav vertebrar of a crossopterygian, the principal central element is a large intercentrum, wedges shaped in side view, cross-centic if seen in end view; there are small paired pleurocentra, B. Vertebrar by the most primitive known amphilian type, of similar construction. C. The typical Thachicomous processors are supersymmetric properties and the properties of the properties of the processors are designed and the intercentrum forms the entire centrum. E. The embodonities the pleurocentra have designed and the intercentrum forms at entire centrum. E. The embodonities of the pleurocentral have supported and the intercentrum forms the entire centrum. Enter the function of the properties of

the centra are short cylinders, formed in the main of concentric layers of cartilage (frequently calcified). These layers are interrupted, however, dorsally and ventrally on either side, by "plugs" of cartilage which underlie the attachments of neural and hemal arches (the latter represented in the trunk by ventral ribs). In bony fishes these same arch bases are present in early stages as distinct structures, but in well-ossified forms such as Amia and the teleosts they are fused at maturity with the remainder of the centrum (Fig. 103, C-F), In the line of fossil forms leading to land vertebrates ossification in the centrum seems to have been concentrated in these arch bases (Fig. 104). In the ancestral crossopterygians and in many of the ancient labyrinthodont amphibians we find a type of centrum in which the dorsal arch bases are present as a pair of small pleurocentra situated high up, close to the base of the neural arch. The fused ventral arch bases of the two sides form a large element, which is wedge-shaped when seen laterally, crescentic in front or back view; this structure appears to be identical with the small intercentrum which we have seen in amniotes. As indicated in Figures 104 and 105, most of the ancient fossil labyrinthodonts tended to expand the intercentrum into a still larger structure as the sole central element. But in the line leading to the reptiles, on the other hand, the intercentrum underwent reduction toward the amniote condition of small size or complete reduction. In this line toward higher

vertebrates, the two pleurocentra become fused and greatly expanded to become the true centrum of amniotes.

Embarrassingly, we cannot readily fit into this otherwise clear story of tetrapod vertebral development the conditions seen in the modern amphibian orders (Fig. 103, G, H). The centra are essentially simple cylinders (despite irregularties in outline) in which there is no evidence of separate structures corresponding to pleurocentra and intercentra. In urodeles and apodans the centra ossify directly, with little or no preceding cartilage formation; in frogs and toads there

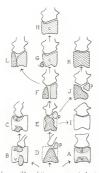


Fig. 105. Diagrams to show possible evolutionary sequence in the structure of vertebral centra. d and v are the dorsal and ventral arch bases found in many fishes, parts of the centrum structure supporting neural arches and hemal arches or ventral ribs, respectively. In crossopterygians and many tetrapods the arch bases appear to be represented by pleurocentra (p) and intercentra (i). Cartilage stippled; arch base cartilages, heavy stipple; pleurocentra hatched; intercentra cross-hatched; parts of central ossifications not included in arch bases, plain white. Part or all of the neural arch is shown as well as the central structures. Front end of vertebrae to left. A, Shark condition; arch bases incorporated in cartilaginous centrum. B, Embryonic Amia vertebra, showing presumed basic actinopterygian condition, with arch bases forming separately from rest of cartilaginous centrum. C, Teleost condition; centrum ossified, and incorporates dorsal arch base and in some cases ventral arch base as well. D, Crossopterygian condition, probably basic for tetrapods; much of the centrum was persistently cartilaginous, but small paired dorsal arch bases ossify as pleurocentra, and ventral elements fuse as a wedge-shaped structure. E. Oldest known amphibians, similar in structure to crossopterygians. F, Type leading toward reptiles among fossil labyrinthodonts; the pleurocentra have grown and fused to form a ring-shaped "true centrum. G. Primitive reptiles; the centrum has grown at the expense of the intercentrum, which is much reduced. H, Advanced reptiles, birds, mammals. The intercentrum disappears, and the whole centrum corresponds to the expanded pleurocentra. I, Modern amphibians; the centrum ossifies as a simple spoolshaped structure, with no evidence of arch bases. J. Structure in rhachilomous labyrinthodonts; the intercentrum is a large wedge-shaped structure, the pleurocentrum persistently small. K, Late, stereospondylous labyrinthodonts; the pleurocentra vanish, and the intercentrum constitutes the entire centrum. L. Extinct embolomerous labyrinthodonts; both pleurocentra and intercentrum form complete rings.

is formation of a cartilaginous centrum to a variable degree, but the adult centrum ossifies in continuity with the neural arch.

Regional Variations in Vertebrae. In higher vertebrates there may be distinguished various regions along the length of the vertebrat column, mainly recognizable through the presence and absence of ribs or changes in the nature of the ribs. But in lower vertebrates ribs may be present on every vertebra from neck to tail without break, and we can do little except distinguish posteriorly a caudal series where, in contrast to the trunk, typical hemal arches are present vertrally. In land vertebrates the attachment of the pelvic gridle to the backbone establishes a sacral region interposed between presacral and caudal segments. In the neck of land forms (as noted later) the ribs tend to be short and may be fused or absent, and there is thus established a ceruical region distinct from the dorsal region of the trunk. In the trunk the posterior ribs became shorter, and ribs are absent here in mammals, so that the trunk vertebrae can be divided in that class into the rib-bearing thoracia and ribless lambars series. Thus there can be progressively established, as we "climb the tree" of the vertebrates, a series of subdivisions as follows:

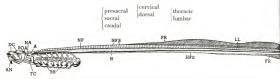


Fig. 106. Skeleton of the lamprey, Petermynon. A, Otic capsule, AN, ring cartilage surrounding mouth; BB, cartilages of branchial basket; DC, dorsal cartilages of mouth region; FR, dermal fars; HFS, fibrous sheath around dorsal aorta; LL, longitudinal ligament connecting fips of neural processes; N, notechord; MA, openings of ansal capsule; NFS, fibrous sheath of spinal cord; YP, neural processes; O, openings of glid thambers; SOA, cartilaginous arth around orbit; TC, tongue cartilage, Grom Dean).

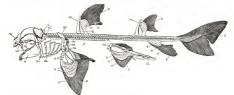


Fig. 107. Skeleton of a shark (Cestracion). A Anal fin; AC, auditory capuale; R basal elements of fin; BB, basibranchial; C, caudal fin; CH, ceratobyal; CL, claspers of male; D, dorsal fins; D', dermal rays of fin; EB, epibranchial; FS, fin spines; HM hyomandibular; ED, bailet cartiliages; M, mandibler NC, assal capsule; O, orbit, FP, peteroral fin; FB, pharyngobranchial; FC, pelvic girdle; FQ, palatoquate; R, radial claments of fin; R', riks, SC, sectoral grifle; F, pelvic (return) fin; (From Deam)



Fig. 108. Skeleton of a teleost (Perca). The interpretation of certain skull elements differs from that used in Figure 157, but is no commond used in works on teleosts. A, and ling, A', aricular, A', angular, B, pelvic girdle; B', skeleton of pectoral fine BS, branchiostegal rays, C, caudal fine, C', centum of vertebus; CB, certabolyal, D, doest line (satterior one supported by stoat derma) simpel; D', dermal rays of fine; B'', dentary; E, ethnoid; EPC, epiotic; FR, frontal; CB, hypobranchia [dassolval); HM, Kupo nandibular; BB, bennal spine; D, dermetopercular (gatar of opercular series); MX, maxillar, NC, top on note-hord in tail; NS, neural spine; D, opercular; P, pectoral fine PA, pariesti, PF, perforant; PM, PC, propercular (gatar of opercular series); PS, supporting processes of rinks, PF, PT'', homes of palatin region; PTE, postfrontia; PTO, percoic; Q, quadrate R, ribs; R', supports of discussion; SC, victoral; NC, suppose copital; SCO, subport-voltar; SOC, suppose-cipital; SOR, subor-tituls; SO, squamosal; UH, urobyal (ventral element of branchial skeleton); P, celvic fin. (From Dean).



Fig. 109. The skeleton of a salamander, as seen from above. (From Schaeffer.)

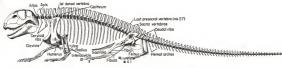


Fig. 110. The skeleton of a generalized primitive reptile (the Permian pelycosaur Haptodus).



Fig. 111. The skeleton of a bird (the pigeon). (After Heilmann.)

As regards numbers of vertebrae, the total is highly variable in fish (Figs. 106–108), but primitive amphibians appear to have had thirty or so presacral vertebrae (of which about seven were cervicals), a single sacral and half a hundred or more caudal elements. Among modern amphibians the wormlike Apoda may run up to 200 or more vertebrae, while on the other hand urodeles (Fig. 109) have a relatively short column, and typical frogs have but nine vertebrae plus a rodlike arostyle representing fused caudals. Primitive reptiles (Fig. 110) had about twenty-seven presacrals, two sacrals in most cases, and a long tail; there is great variation within the class, with snakes having a greatly lengthened column. A curious condition is seen in the tail of Sphenodon and various lizards, where there is a "breaking point" in the middle of each caudal at which the tail may be shed. In birds (Fig. 111) the cervical region is distinct and variable in length; the trunk vertebrae tend to be fused, and the sacral region has added to it posterior dorsals and anterior caudals to form an elongate synsacum. The short bony tail of a brit terminates in a pygostyle formed of fused vertebrae.

In mammals (Fig. 112) the cervical region contains almost uniformly seven vertebrae. The number of dorsal vertebrae is usually in the twenties and tends to be stable within many mammalian families or even orders, but the number of ribs—and bence the proportion of thoracies to lumbars—is variable. The mammalian tail is generally a slender and relatively short structure.

In fishes, head and trunk move as a unit, but in land vertebrates independent head movement is important, and usually the first two vertebrae—the adias and axis—are specialized for this purpose. In typical amphibians the articular surface at the back of the skull—the condyle—is divided into a pair of rounded prominences, one at each side. The allas correspondingly has a pair of sockets, and the head can swing up and down readily, although there is little facilitation of side-to-side movement. In most reptiles and birds the condyle remains single, but atlas and axis (Fig. 113) are modified to permit flexibility of movement. The

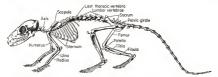


Fig. 112. The skeleton of a generalized mammal, the tree-shrew, Tupaia. (After Gregory.)

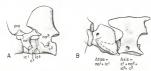


Fig. 113. The atlas-axis complex. A. The occipital condyle and first two vertebrae in a primitive reptile (Ophiacodon). B. The same region in a typical mammal, showing fusion of elements. The protable in I is the neural arch of a "but" vertebra of which the centrum has fased with the occipit. The broken line in B shows the position of the odostoid process (c<sup>2</sup>), which runs forward inside the ring of the atlas. c<sup>2</sup>, c<sup>2</sup>, Centrum of first and second vertebracy; c<sup>2</sup>, c<sup>2</sup>, intercuting ca<sup>3</sup>, and, neural arches; poor, promote the contraction of the contrac

atlas neural arch and intercentrum may form a ring on which the head may turn to some degree; and in mammals with two condyles the atlas centrum fuses with the axis as its odontoid process, which lies inside the atlas ring and aids in rotary head movements. The axis generally has a strong neural spine for attachment of ligaments supporting the head.

The powerful segmental trunk muscles of fishes are their main locomotor organs, forcing the body ahead by alternate contraction and consequent undulation of trunk and tail. Their force is exerted upon the connective tissue septa-myocommata-between successive segments; ribs, formed at strategic points in these septa, connect with the vertebrae and render the muscular effort more effective. In most fishes each muscle segment is divided into dorsal and ventral parts by a longitudinal septum (Figs. 2, C, D, p. 7; 114). A logical place for rib formation is at the intersection of this septum with successive myocommata; in some fishes dorsal ribs develop at this point, and the ribs of tetrapods appear to be of this type. A second position in which ribs may form is that where the myocommata reach the walls of the celomic cavity. Such ribs, common in fishes but absent in land vertebrates, are termed ventral ribs. At the back end of the trunk in fishes the ventral ribs of the two sides approach one another and a bit farther back form V-shaped structures, which are the hemal arches already described as connected with caudal vertebrae. The ribs develop as cartilages but, except in the sharklike fishes, are generally ossified, fully or in part.

In tetrapods the ribs were primitively borne, as in fishes, on every vertebra from neck to tail base. The cervical ribs in the more generalized lower tetrapods are relatively short, in relation to the development of a flexible neck; the thoracic

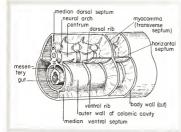


Fig. 114. Diagram of a section of the truto of a vertebrate to show the connective tissue system and the axial sketcal elements. A view from the left side, as if partially dissected out and the muscles removed from between the septa. Vertebral elements develop in the tissue elements develop in the tissue core and and notherheaft iths, devsal or ventral, develop where the transverse septum interests the horizontal septum or colomic sall. (dhere Goodrich)

ribs, in contrast, are the longest of the body and are generally bound to a median ventral structure, the stermun. In the more primitive tetrapost short lumbar ribs are present; following these are one or two sacral ribs, connecting the backbone with the pelvic girdle. Beyond the pelvis, short ribs, diminishing in size posteriorly, may be present in the basal region of the tail. In primitive tetrapods the ribs were double-headed, a capitulum, or head proper, attaching in early forms to the intercentum, and the ubercaulum, an accessory head, to the transverse process of the neural arch (Fig. 100). Posteriorly the two heads became approximated, the capitular attachment shifting upward and backward toward the transverse process. The lumbar ribs, the massive sacrals and the caudals were generally immovably attached to the vertebrae.

Many groups, however, have in many respects departed far from this primitive pattern. Ribs are much reduced in the recent amphibian orders, never reach the sternum, and except for a single sacral are generally absent in anurans. In reptiles the rib is frequently single-headed and may attach to either centrum or neural arch. In turtles the ribs are reduced in number, eight of them are firmly fused to the carapace. In birds the exercical ribs are fused to the vertebrae; free ribs are confined to the short thoracic region, and the pelvic girdle is supported by a long sacral series. In mammals cervical ribs appear in the embryo in the neck region, but in the adult they are fused to the vertebrae; ribs are absent from both lumbar and caudal regions.

Sternum (Figs. 115, 124, B, E, F, p. 153). In the generalized condition seen in many reptiles the sternum is a ventrally placed shield-shaped cartilage which articulates anteriorly with the shoulder girdle and posterolaterally connects with the ventral ends of thoracic ribs to form a complete enclosure of the chest region. No such structure is present in fishes. In modern anurans and unodeles a sternum is present but does not connect with ribs; in the frogs it frequently develops in rodike form. With limb and girdle reduction, the sternum disappears in the apodous amphibians and snakes; in chelonians its absence is associated with the development of the plastron.

In birds the stemum is enormously developed for the attachment of massive

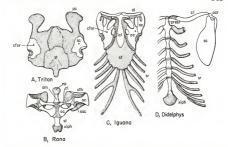


Fig. 115. Ventral views of the shoulder girdle and sternal apparatus in various tetrapols. For lateral views, cf. Figures 123 and 124 (pp. 152, 153a). As, Shamader R, a frequ. 6, a liared, P, a missing loposum), Anterior cend at the top of the figures. In A and C the descally turned scapulae are invisibles. In A the two consolid cartilages overlaps, as indicated by the benken line, α. Anterior consolid crisibles or according cfor, concoid foramer, cf., clavicle cth. cleithrame qs. painternam; icf, interclavicle que, or, accommon, for concoid foramer, cf., clavicle cth. cleithrame qs. painternam; icf, interclavicle que, monitorium; pp. precoracior diregion of concord plate; pers, presternam; x, scapula (in salamaders this constituction extends down into the place of the absent concoidly ss, sternal ribs, are, suprascapula; x, sternam; ps. A. phistorrum, Cartillog salppled, L. (z. and D after Parker).

chest muscles, important in flight, and in all except the flightless ostrich-like forms bears a huge ventral keel for additional muscle attachment. In mammals the sternum is typically an elongate, jointed rod with which the ribs are attached at the "nodes."

Brainease. The brainease, of cartilage or replacement bone, forms the anterior end of the axial skeleton, here greatly modified in relation to the expanded brain and special sense organs. In most vertebrates the brainease is fused with dermal and visceral skeletal elements to form a definitive skull structure; in sharklike fishes and cyclostomes, however, it is a separate entity because of the absence of dermal bones—presumably a secondary condition. The cartilaginous shark brainease (Fig. 116) shows a structure which, with variations, is repeated in many other lower vertebrates (although in them usually ossified, at least in partly; in modified form it is represented in the skull of even the highest of vertebrate groups.

The most posterior part of the shark braincase is relatively narrow. There is a median opening, the foramen magnum through which the spinal cord passes, and below it a circular occipital condyle which abuts against the centrum of the first vertebra. Anterior to this the braincase expands, there is here incorporated on either side an otic capsule, containing the sacs and canals of the internal ear. Farther forward the width contracts to allow the formation of orbital cavities for the cybelally there, internally, a median ventral depression lodges the pituitary. Toward the front the braincase again expands to terminate in a rostrum, on either side of which is a masal capsule, containing the olfactory organ. Numerous open-

ings—foramine—are present in the braincase for cranial nerves and blood vesels, as may be seen in Figure 116; dorsally the endolymphatic ducts from the internal ear (cf. Chap. 15) open to the surface in sharks (but not in other groups), and ventrally there enter the carotid arteries which supply blood to the brain. A specialized gill blar element propping the jaws—the hyomandibular—articulates loosely with the outer side of the otic region, and the cartilages which form the jaws also articulate with the braincase (Fig. 150, p. 174). The common jaw connection in modern sharks is one in which the upper jaws are loosely joined anteriorly with the under surface of the braincase, in primitive sharks there is an additional articulation posterior to the orbit. In higher fishes and primitive land vertebrates this latter connection tends to be reduced or absent, and there is, instead, a strong basal

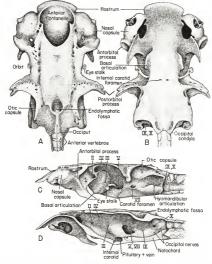


Fig. 116. The braincase of the shark Chlamydoselache; A, dorsal, B, ventral and C, lateral views, and D, sagittal section. Nerve exits in Roman numerals. (After Allis.)

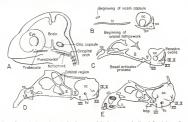


Fig. 117. Stages in the embryonic development of the braincase of a kizacl. In d the outlines of the head, brain, and notochord are given for orientation. The main elements of the braincase structure are appearing—traheculae, parachordals, oftic capsule, and occipital arches (the nasal capsule appears lister), trainted-evelopment consists in great measure of the growth and fusion of these elements. In the linear function of the contraction of t

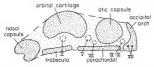
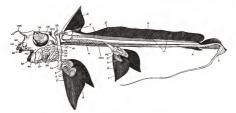


Fig. 118. Diagram to illustrate the main embryonic components in the formation of a braincase. Tablesulae and parachockals are the main ventral elements to which an occipital arch (or arches) is added poteriorly. Usually latter in development are more dorsal elements: ofic capsule, massl capsule and orbital plate (the last, as in Fig. 117, often develops merely as a latticework). These primary elements are later bound together by a further growth of cartilage, leaving, however, gaps for nerves and blood vessels.

articulation of the upper jaw and palatal structures with the base of the braincase in the orbital region (Figs. 117, £; 151, B, D, E, p. 177; 152, p. 178; 157, p. 183; 170, p. 193).

In the embryo vertebrate (Figs. 117, 118) both the brain and the notochord, which extends forward beneath it to the pituitary region, are already far advanced in development before skeletal structures appear. Basic cartilage elements of the braincase are a pair of parachordals which lie on either side of the notochord beneath the brain stem and, farther forward, the trabeculaer—paired in most vertebrates but a single bar in mammals. Above the parachordals on either side, the otic capsule develops as a shell of cartilage around the internal ear. Behind the otic capsule one or several modified vertebrae form occipital arches; in front, between the orbits there may develop a pair of orbital plates or a lattice of cartilage hars as a substitute for them. At the front end the nasal capsules presently make



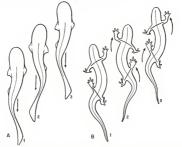


Fig. 120. 4. Doral view of a fish swimming, to show the essential method of progression by the backward thust of the body on the water, resuling from secessive waves of curvature tracelling backward along trunk and tail. The curve giving the thrust (indicated by arrow) in t has passed down the tail in 2 and is replaced by a succeeding wave of curvature, the thrust of this wave carries the fish forward to the position seen in 3, and so on B. Borsal views of locomotion in a salamander. Although timbs are present much of the forward progress is still accomplished by through the body into successive waves of curvature. In position 1, the right front and left hind feet are kept on the ground, the opposite feet raised, a swing of the body in 2 curries the free feet forward, as indicated by arrows. Here feet are now planted and the other two raised, a following reversed swing of the body will carry them forward another step, as seen in 3.

their appearance. In later stages all these structures fuse with one another to form the adult braincase, but leaving between the original units spaces for the various nerves and vessels which enter or leave the braincase. In cyclostomes the braincase (Fig. 147, A, p. 172) is highly aberrant. The short, high chimaera braincase (Fig. 119) has as a notable specialization the fusion with it of the upper jaw cartilages, and the same peculiarity is repeated in the lungfishes.

Median Fins. In primitive water-dwelling vertebrates the body shape is most generally a fusiform one but with a side-to-side flattening posteriorly. This flattening is associated with the nature of the propulsive force. Forward motion is produced by side-to-side movements of the body effected by the axial muscles (Fig. 120, 4). Alternating curves, successively produced on opposite sides, travel back along trunk and tail, pushing the body forward as a result of their backward thrust, with accentuation at the expanded caudal fin at the posterior end of the body.

Without the aid, in stabilization and steering, of fins other than the caudal, these propulsive movements would tend to be essentially unregulated (as are those of a tadpole). Further median fins in addition to the caudal are, above, dorsal fins—usually one or two of them—and an anal fin below, posterior to the anus. The skeleton of the median fins is formed in the dorsal median septum in which the neural spines are formed, and in the tail placed in the ventral septum in which the hemal arches occur. In the caudal fin neural and hemal arches may themselves contribute directly to fin support (Fig. 121), and in teleosis the terminal hemal arches are expanded structures termed the hypurals. In the case of dorsals and anals, however, such direct support is not present, the fins are stiffened by radials (sometimes in two rows), which may articulate at their bases with neural or hemal arches but are often separated by a gap from these structures (Figs. 107, 108, 119; pp. 140, 141, 148). Primitively, it appears, the radials

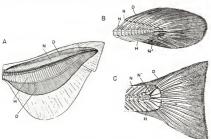


Fig. 121. Caudal fins. A, Heterocercal type seen in sharks, sturgeons, puddlefish; B, diphycercal type, as seen in Polypterus; C, homocercal type of teleosts. Abbreviations: D, Dermal fin rays; H, hemal spines; N, neural arrches; N', tip of notochord; R, fin radials. In C, enlarged elements beyond H are hypural bones. (From Dean.)

extended well into the fin, as is the case today in sharks; in actinopterygians, however, they hardly extend at all into the free fin, which is supported mainly by lepidotrichia (cf. p. 133). In a number of sharks and in chimaeras the median fins carry, anteriorly, spines which act as cutwaters, and spines were present on median fins in the fossil acanthodians (Fig. 20, A, p. 40). In some of the lowly ostracoderms (Fig. 18, p. 38) we find rows of dorsal spines acting as stabilizers, and it is possible that such spines were the basic structure from which median fins were historically developed.

Of caudal fins, three major types are to be found in fishes. The heterocercal fin type is that familiar in sharks (Figs. 21, 22, A, B, pp. 41, 42; 107, 121, 4); the tip of the body turns upward distally, and the greater part of the fin is developed below it. This type of tail is also found in many placoderms (Fig. 20, p. 40), on the one hand, and in all the more ancient bony fishes on the other; it is retained today in Osteichthyes, however, only in sturgeons and paddlefishes (Figs. 27, A; 28, A; 29, A; 30, pp. 47, 48, 49, 50). The dominance of this tail fin structure in so many primitive and ancient fishes strongly suggests that it is the ancestral vertebrate type. Its only rival for antiquity is a recersed heterocercal type, seen in some ostracoderms (Fig. 18, B, p. 38) and retained in larval lamorevs.

A diphyceral In type is one in which the body axis runs straight outward to the tip of the tail, with the caudal fin developed symmetrically above and below it; good examples are seen in Polypterus and the living lungfishes and coelacanth (Figs. 27, B; 28, B; 29, B; pp. 47, 48, 49, 121, B). At first thought one would expect that such a structure would be the true primitive type of tail fin. But in almost every case it can be shown that this symmetric fin is derived from a heterocercal type. Both Polypterus and the modern lungfishes come from Paleozoic ancestors with a heterocercal tail; many crossopterygians (including the living form) developed symmetric tail fins, but the most primitive members of that group exhibit the heterocercal structure. Skates, rays and chimacras have in general slender, rather whiplike tails of symmetric build (Figs. 21, C; 22, pp. 41, 42), but intermediate stages are known which connect them with heterocercal types.

The third major tail type is the homocercal fin characteristic of the dominant modern fishes, the teleosts (Figs. 32, 33, pp. 52, 53; 108, 121, C). This is superficially symmetric, but dissection shows that the backbone tilts strongly upward at the tip; the fin expanse is purely a ventral structure. Among fossil and recent actinopterygians a whole series of forms are known which show the derivation of this fin from the heterocercal type of the ancestral ray-finned fishes. Intermediate forms are known among the holosteans, such as the gar pike and Amia (Fig. 31, p. 51). In these fishes the tail is nearly symmetric in external form but clearly shows in internal structure that it has arisen by an abbreviation of the uptitled axis of a heterocercal tail.

In land vertebrates, except for a few very primitive fossil amplibians, the original median fin structures of fishes have been completely abandoned; even in the swimming tail of a tadpole or salamander the skeletal supports found in their fish ancestors are absent. Many tetrapods have returned to an aqualic existence but often—as in seals, turtles and the extinct plesiosaurs—limbs rather than a tail act as propulsive organs. Among mammals the ectaceans and sea-cows have a tail "fin," but this consists of horizontally expanded flukes and is not closely comparable to a fish caudal fin. The extinct ichthyosaurs have come the closest to the redevelopment of a fish type of tail, expanded vertically and supported by

Fig. 122. Baculum of an otter,



the axial skeleton; the tail is of the "reversed" rather than the typical heterocercal type, however.

Heterotopic Elements. Embryonic connective tissues are the source of the normal skeletal tissues, and it is hence not surprising that here and there among the various vertebrate types there develop upon occasion cartilages or bones in situations where mere connective tissue is normally present. Small bones—sesamoids—may develop along the course of tendons, and the mammalian knee cap is an overgrown example of such an element. Bones may develop, for example, in the eyelded of crocodiles, in the hearts of deer and hovids, in the expanded muz-les of some mammals. A common mammalian example of such a heterotopic bone is the baculum (os penis), developed in the penis of many mammals (Fig. 122), including insectivores, bats, carnivores and nearly all primates (man is the exception).

## APPENDICULAR SKELETON

The skeleton of the girdles and limbs belongs (with the exception of dermal shoulder elements) to the somatic system of internal skeletal structures, in their history, however, they contrast strongly with axial somatic elements. Normally two pairs of appendages are present, as paired fins in fishes and as the limbs of tetrapods. These are the pectoral appendages, situated in fishes just behind the gills and in land animals in an equivalent position between neck and trunk, and the petic appendages placed at the back end of the trunk, just anterior to anus or closea.

Origin of Paired Fins. Paired appendages were not ancestral vertebrate structures; they are absent in eyclostomes, are only rarely seen in the early jawless ostracoderms and are poorly developed in many of the ancient placoderms. The mode of origin of paired fins has been much debated. One early theory assumed that they developed from modified gills—that the limb girdles are transformed gill bars and that the limbs themselves developed from gill flaps such as lie outside the gill surfaces in a modern shark. A host of embryologic and morphologic facts show that this idea is purely fanciful; but a reminiscence of this theory remains in the name archipterygium (p. 159) given to a leaf-shaped fin type (Figs. 129, H, p. 159; 130, D, p. 160) which was supposed, under this theory, to be primitive that aponeared is in oth.

In reaction against this theory arose a rival finfold theory of the origin of paired fins. Its advocates pointed out that the paired fins are basically similar to the median fins in structure and hence may have arisen in similar fashion. In either case the fin has a centrally placed set of skeletal structures with a layer of muscle on either side. The median fins appear to have arisen as stabilizing organs in the midline and the paired fins may have been, originally, laterally projecting stabilizing flanges; only later, it would appear, did they become flexible steering organs, and in few forms below the tetrapod level have they any active

role in propulsion. In ostracoderms (Fig. 18, p. 38) we find some early essays toward paired fin development, such as rows of spines extending out from the base of either flank or as projecting flaps comparable to pectoral fins. In the extent placoderms paired fins, we have noted, were still "experimental models" in which spines were generally differed as much from the more orthodox fins of later date as did many early (and unsuccessful) thing machines from the modern airplanes. There was even variation in the number of these appendages, with as many as seven pairs in one "spiny shark." It is not until we reach the more "modernized" fishes, such as the sharks and Osteichthyes that there developed typical fish fins, flexible in nature and two-paired in number.

Pectoral Girdle—Dermal Elements (Figs. 123, 124). Each limb has, in addition to the free appendage, an associated girdle lying within the trunk and affording support to the limb skeleton as well as an area of origin for limb muscles. Each girdle consists primarily of endoskeletal cartilage or of bone replacing it. The shoulder, however, lies in the anterior region of the body in which, in

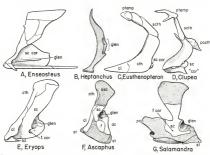


Fig. 123. The shoulder girdle in fashes and amplihians. A, Devonian placederm, R, a shark, C, Devonian crossoregians, D, a sleeck (herring); E, a Placesoic primitive amphisians, F. a frag, C, a salamander. Cartilage stippled. In all except B and G a dermal girdle is present in finishes A, C, D, this is the most prominent part of the girdle, including all parts except that labeled scapuls and coracoid, and in the placederm (A) the dermal girdle is the lateral part of an extensive thoracic armor. In amphibians the dermal girdle is reduced or absent. Except in the shark the endosketel girdle is reducedy small in tables and partially hidden beneath the dermal elements. In amphibians the candoxicating girdle is reproduced as single center, comparable to the sample of aministes the frag, expanded, but generally consists from a single center, comparable to the sample of aministes the frag, expanded and the control of the control

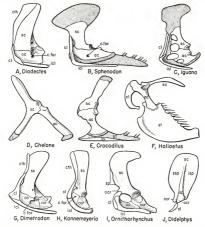


Fig. 124. The shoulder girlle in reptiles and mammals. A. "Stem reptile" (cotylossury): E. Sphepologic, G. Inizard, b. a nutrie; E. a croscodile; F. a bird, G. a phevosaur (primitive mammal-like preptile); H. a therapoid; I. a monstreme (duckbill); I. opossum. In B. E. and F the sternum is shown. In most reptile and birds only one (unterior) coroxoled element is present; in mammal-like forms the true coroxold appears and persists, despite the loss of the coracoid plate area. The borders of the scapula and coroxold are often cartilaginous in reptiles. In lizards, separal and corocoid are often enterstated at points of muscular origins. The cleritum has vanished in all living ammiests, but persisted long in mammals for muscular origins. The cleritum has vanished in all living ammiests, but persisted upon the sequal area of the scapular in monotreme, but hack of the new supraspinous fosas in higher mammals. α. Anterior coracoid: orthe of reptiles, birds, monotremes, ασ. acromion; α. (for, coroxolió forment; c) claricles (ασ. true coracoid: αΛ, cleirtum; ιξι. interedavicle: 1ρs, infraspinous fosas; κ., scapula; 1ρs, spine of scapula;

early fishes, bony plates were present rather than the small scales covering most of the trunk and tail. Certain of these plates became associated with the limb supports as a dermal shoulder girdle. This is present in all jawed fishes, except for the sharklike forms in which all bone has been lost.

Most placoderms, we have noted, had a bony armor surrounding the "chest" region, and the later portions of this armor form essentially a dermal shoulder covering, although the elements present are not comparable with those of higher types. In all primitive bony fishes a characteristic pattern of dermal elements is 154 THE VERTEBRATE BODY

present. Ventrally on either side is a small claricle, homologous with the familiar "collar bone"; above it in fishes is a much larger element, the cleithrum, and still farther dorsally one or more further elements extend upward and forward above the gill chamber to attach to the posterior margin of the skull. This type of girdle is characteristic of all crossopterygians and lungishes. It was also present in the older ray-finned fishes and persists today in the more primitive living members of that group. Advanced actinopterygians, however, lost the clavicle, leaving the clithrum as the sole external covering for the endochondral girdle beneath.

In primitive land vertebrates both clavicle and cleithrum persisted; however the connection with the head was lost (allowing greater freedom of movement), and the bones were no longer broad plates but relatively narrow structures attached to the front margin of the internal girdle for most of its height. There was, however, a new development in the presence of an interclavicle, a median ventral plate of bone to which the expanded lower ends of the clavicles attached. In later land vertebrates the dermal elements have had a varied history, as may be seen from Figure 124. On the whole, the story has been one of reduction. The cleithrum, it would seem, became "unfashionable" at about the beginning of the Age of Reptiles, and today the only relict of this once important bone is a sliver which may be found at the upper front margin of the anuran shoulder girdle. Urodeles and apodans, snakes and many mammals have lost the entire girdle. The interclavicle persists in many reptiles and in the primitive egg-laying mammals but is otherwise absent. The clavicle has been more persistent; it is found in anurans, lizards and Sphenodon and in a large proportion of the mammals. The fused clavicles form the furcula, the "wishbone," of birds. In chelonians the clavicles and interclavicle, as we have noted, have been incorporated in the shell.

Endoskeletal Shoulder Girdle (Figs. 123, 124). Functionally the endoskeletal girdle is more important than the dermal component, since it always
bears the limb articulation and offers an area of attachment for limb muscles. It
is persistently cartilaginous in the Chondrichthyes but normally is partially one
completely ossifed in other fishes. The ossifications present in fishes are some
what variable and need not concern us here, but the general pattern of endochondral girdle construction seen in bony fishes is comparable to that seen in tetrapods. Centrally situated on either side is a socket, or series of sockets, for articulation with the skeleton of the appendage; when—as in some fishes and all
tetrapods—there is but a single element articulating here, this socket is termed
the gelenoid fossa. Above this point is a sheet of bone or cartilage, more or less
covered by the dermal girdle, which may be termed the sequalar blade; below
the fin articulation, and deep to the plane of the lower part of the dermal skeleton, is the concoid plate.

In primitive land vertebrates this bony fish structure is essentially retained. But whereas, we have noted, the dermal elements are here reduced, the endo-chondral girdle is greatly expanded—this in relation to the increased areas of muscle tetrapod limb and its need for stronger support and for increased areas of muscle attachment. In primitive amphibians the entire endochondral girdle ossifies as a single element which comparative studies show is the scapula of later types. In anurans and reptiles a second, ventral ossification appears, restricting the scapular ossification to the blade above the glenoid cavity. This lower element in frog and reptiles is frequently called the coracoid; but as will be seen shortly, this lone is not the same as the true coracoid of mammals and is better termed anterior coracoid or presconsoid.

In reptiles and birds an endochondral girdle formed of these two elements is generally present, although with considerable variation in shape from group to group. In the fossil forms leading to mammals, however, there is a new development. A second element, the true coracoid, appears in the coracoid plate at the back and gradually, in the therapsid reptiles, usurps the place of the anterior coracoid (Fig. 124, G-I). The egg-laving monotreme mammals have a shoulder girdle resembling fairly closely that of their reptilian ancestors. In the transition to the marsupials and placentals, however, there is a striking change. The entire coracoid plate of lower tetrapods disappears, leaving of the girdle only the scapular blade above the glenoid fossa and a tiny projecting "crow's beak" at its lower edge representing the coracoid. Further, the scapular blade is a double structure. with a scapular spine running down the middle to end ventrally at the projecting acromion for attachment of the clavicle. Consideration of the evidence shows that this spine represents the front edge of the ancestral scapular blade and that the surface in front of (or above) the spine is a new development. The answer to the question as to the functional "reason" for these major changes in girdle construction is to be found in marked changes in limb musculature (cf. Fig. 186, p. 212).

Petric Girdle (Figs. 125–128, 130). In fishes the pelvic girdle is of very modest size; essentially each girdle half is a wedge-shaped element, frequently carrilaginous, which lies in the connective tissues of the fish's belly. It is with-

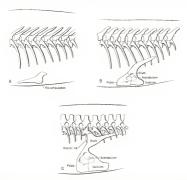


Fig. 125. Diagrams to show the development of the pelvic girlle and sacram in the colution of am and publishin from indexes, A, Left lateral lives of the pelvic region of a fish, with the vertebral column arise above, the small pelvic girlle placed ventrally. B, Primitive tetraped stage, found in some carly food all amphilians. The girlle has expended, with the three typical boys elements. The litum cutends upward, but was presumably connected with the column only through lingments binding it to the neighboring risks. C the girlle has grown further, and the litum is furnly attached to a nealized scaraff ling risks. C the girlle has grown further, and the litum is furnly attached to a nealized scaraff ling risks. C the girlle has grown further, and the litum is furnly attached to a nealized scaraff ling risks.

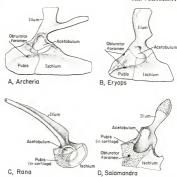


Fig. 126. The pelvic girdle in amphikians. A. A primitive fossil labyrinthodon; B. a typical later labyrinthodon; C, a frog. D, a urodele. A posterior process of the illum, present primitively, is retained in many reptiles (cf. Figs. 127 and 128), but is lost in most Amphibia (represented by a prong in B). In the anarrass the illium is a specialized and eloogute rod. The public was primitively well ossified, but remains cartiliganiss in marpfossil forms and all modern amphibians.

out attachment to skeletal elements of the body; the girdles of the two sides, however, usually meet one another medially in a pelvic symphysis.

In tetrapods, with powerful pelvic limbs, the pelvic girdle increases greatly in size; further, it is imperative that the girdle gain a connection with the axial skeleton to "anchor" the limbs. The ventral portion of the girdle expands into a large plate, affording a broad area for limb muscle attachment; this plate includes two ossifications, the pubis anteriorly, the ischium posteriorly. A common landmark is the obturator foramen piercing the pubis and transmitting a nerve to part of the limb muscles. At the summit of this ventral plate is a socket, the accubulum, into which fits the bead of the thigh bone. Above the acetabulum rises a portion of the girdle not known in fishes, which extends upward to gain a firm connection with the backbone through the development of sacral ribs and usually expands in blade-like fashion to afford an area of dorsal attachment for limb muscles. This dorsal portion of the girdle is formed by a third element, the ilium.

Except in cases in which limbs are reduced or lost, the essential structure of the pelvic girdle persists in most tetrapods. In modern amphibians the pubs fails to ossify, and in the anurans the ilium becomes an elongate rod in relation to the shortening of the backbone of these forms. Among reptiles there are modifications of two types usually present in the ventral plate of the girdle. In Sphenodon, lizards and turtles a large opening, frequently termed a thyroid (i.e., heart-shaped) (nestra develops in this plate for the better functioning of a large

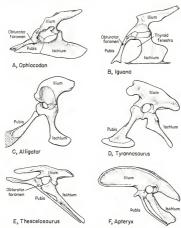


Fig. 127. The pelvic girdle in reptiles and birds. A, Primitive reptile; B, a lizard; C, a crocodilian; D, a reptile-like dinosaur (Saurischia); E, a birdlike dinosaur (Ornithischia); F, a bird (the kiwi). In A the ilium is a low blade, and the same is true in lizards; in other forms this structure is more expanded. In the dinosaurs and birds, with a bipedal type of locomotion, the ilium has grown forward somewhat as in mammals (cf. Fig. 128). In the archosaurs (C, D, E) and the birds descended from them there is typically an open bottom to the acetabulum for the better reception of the head of the femur. In the primitive reptile the pubo-ischium is a solid plate. In lizards there is a large thyroid fenestra developed between pubis and ischium, from which a large muscle to the femur takes origin (Sphenodon and turtles are similar). This fenestra is comparable to one seen in mammals, but there the obturator foramen is concerned in the development of the fenestra. In such archosaurs as the allieators and saurischians there appears at first sight to be a similar structure. Actually, however, this is not the case; the pubis and ischium are twisted downward, and the true ventral margin of the girdle is the curving lower margin of pubis and ischium. In C and D the pelvis is triradiate, with a simply-built pubis; in E the pubis is twopronged, and the pelvis tetraradiate. In the bird the anterior process of the pubis is reduced or absent. In the alligator the pubis is excluded from the acetabulum by the ischium; the pubic region of the girdle extends forward along the belly as a fibrous cartilage.

limb muscle originating from this area. In the crocodiles and many dinosaurs (Fig. 127, C, D) the plate is modified in another fashion. In the primitive members of the archosaurs (the major group to which these reptiles belong) there was a strong trend toward a bipedal gait, and it appears to have been advantageous, for better

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working of the limbs, that muscles attach to the anterior or posterior ends of the plate rather than the middle. In consequence, the ends of pubis and ischium are elongate and turn downward, and the middle part of the plate is narrow, giving the girdle a triradiate structure. In one group of dinosaurs (the so-called birdlike forms) and in the bird descendants of the archosaurs there is a further modification (Fig. 127 E, F); the pubis has swung back parallel to the ischium. In the dimosaur group with this type of pelvis there has, further, developed a new anterior prong of the pubis which helps support the abdomen; this is absent in birds, where support here is rendered unnecessary by the presence of a large sternum (cf. Fig. 111, D, 142).

In the evolution of mammals (Fig. 128) there has developed a large opening in the ventral plate. This is a parallel to the thyroid fenestra noted in some reputies, here, however, the opening (in contrast to reptiles) includes the ventral nerve foramen in its area and is termed the obtain fenestra. In egg-laying mammals and in marsupials there are present belly supports in the shape of a pair of prepubic bones; there are no such structures in placentals, and they are generally termed "marsupial bones" on the assumption that their function is support of the pouch (marsupium) in which the young are carried.

In the mammalian pelvic limb, as in the pectoral, the musculature has been much modified in connection with a changed posture of the limb, with the effect of giving better placed areas of muscle attachment, the pubis and ischium have

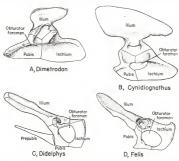


Fig. 128. The pelvie girdle in manual-like repilles and mammals. A, Primitive pelvosaure, B, as the Dimertoon pelvis is of a primitive repilisa type. In the three pairs of the primitive repilisa type. In the three pairs the tiltum has grove forward dorsally, pubis and ischium have swang back ventrally, and the olturation formen has expanded (comparable to the situation in many modern repilies) into a noburator (or thyroid) fenestra. The opossum and cat show a typical mammalian structure, with a large obturator fenestra, as obserted in Schium and a selenct filling (secondarily broadened in many heavy mammals, however, The opossum, like other manupials and the monotremes, has a pair of "marsquial bone" not found in other groups, (in the cat, as in certain other manuals, an accessory element is seen in the activation).

been rotated backward below the acetabulum, the ilium, in contrast moving forward above.

Paired Fins in Fishes (Figs. 129, 130). We noted earlier some of the theories connected with the origin of paired fins. Apart from various peculiar early fossil types, we see in the general run of living and fossil fishes two basic types of paired fin skeletons (together with intermediates). One type is the architeprezium, well-developed in the lungfish Epiceratious (Figs. 129, H. 130, D), in which the fin skeleton consists of a main axis with side branches. This type of fin is present not only in ancient lungfishes but in some of the most primitive crossopterygians, and hence may be primitive for the sarcopterygians as a whole. It is further of interest that in most fossil crossopterygians there was an abbreviated variant of this fin type (Figs. 129, 4, 130, E) which can be interpreted as

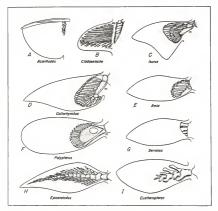


Fig. 129. Pectoral fins of fishes. All are fins of the left side, viewed from the upper surface, so orient data the long axis of the body is vertical on the appec, the anterior end above. The outline of the complete fin is indicated, and (except for A) the articular region of the girdle is included at the right. A. Fossil acambionia, with the fin sketchon little developed, and a spin forming a cutwater and in support. B, Primitive fossil shark, with a parallel-bar type of fin. C, Modern shark with a nurshare fierbile in and a basel concentration of hors with formation of a metapteregal axis the metapteregal axis the entire of the state of the stat

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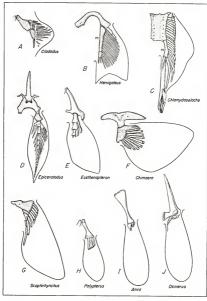


Fig. 130. Pelvic fins of fishes. All are of the left side, viewed from below, the midline of the hori; at the felt, the anterior end above. The fin ostuline is indicated in each case. The left half of the pelvic girdle is included, or the whole girdle if the habres are fused. A, Primitive Carboniferous shark, with roacid-hased in and parallel hars as in support. B, Modern Genale shark, with similar construction. C. Male shark, with additional earthleges supporting the clasper. B. The architection in the Australian and Carboniferon and Carbonife

antecedent to the land limbs of tetrapods. Among fishes, however, the archipterygium is not otherwise known except in one aberrant shark group.

In strong contrast to the archipterygium is the finfold type of fin seen in ancient Paleozoic sharks such as Cladoselache (Figs. 129, B. 130, A). Here the fin has a broad base, and was obviously little more than a horizontal stabilizer, with little freedom of movement. In later sharks and in chimaeras (Figs. 129, C. 130, B. C. F) the base has generally become much narrower, thus allowing greater freedom of movement; the bases of the supporting bars have been crowded together. There is a tendency for a posterior element, termed the metapterygium, to become an axis with which many of the bars articulate; it is probable that the archipterygial fin type has evolved by further development of an axis of this sort.

The actinopterygians are defined as a group in which the fins are mainly supported by horny rays, with the skeleton and flesh restricted to the fin base. The fin skeleton in consequence generally consists of short bars of bone or cartilage at the fin base (Figs. 129, E-G; 130, G-J). These bars are parallel strutures, as in a primitive shark, but (except for such primitive forms as the stugeons) are few in number, so that in consequence the fin usually has a narrow base and consequent flexibility.

In most fishes the pectoral fins are the larger of the two pairs, and in skates and rays they are enormously enlarged. The pelvic fins are reduced or absent in some teleosts, or are moved forward to the shoulder region (Fig. 33, B, p. 53) or even to a position beneath the "chin." In the Chondrichthyes the pelvic fins of males bear finger-like claspers associated with internal fertilization (Figs. 24, p. 44; 107, 130, C).

The Tetrapod Limb. Although the limbs of land vertebrates appear, at fissight, strikingly different from fish fins, the two are comparable in basic structure. Tetrapod limb elements are broadly comparable to those of many crossopterygians, and the complex muscles of a land limb can be analyzed into two opposing muscle groups comparable to those of more simple nature which are present on the upper and lower surfaces of the fish paired fin.

The limb of a primitive land vertebrate is composed of three major segments (Fig. 131). In both front and hind limbs—i.e., pectoral and pelvic appendages—the proximal segment includes but a single bone—hunerus or femur—projecting laterally from the body. Beyond the elbow or knee region is a second segment which is more or less vertically placed. This contains in either limb a pair of elements—radius and ulno in the front limb, tibia and fibula in the hind, the first named in both cases being the more anterior or medial member of the pair. A third segment is that of the foot—manus and per respectively. A proximal portion, which more or less flexibly adjusts the foot on the forearm or lower leg is the wrist or ankle region—carps or tarsus—while beyond are the toes, or digits. The proximal element of a toe (contained in palm or sole) is a metapodial—a metacarpal or metatarsal—while the more distal elements are the phalanges.

This arrangement of limb bones is, as mentioned, comparable to that found in the crossopterygian ancestors of the tetrapods (Fig. 132), in which the fin contains, as in the tetrapod limb, a single element in the first joint and two in the second. Beyond this point known crossopterygians show a variable branching ar-

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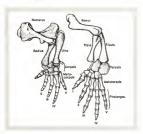


Fig. 131. Left front and hind limbs of a primitive reptile (Ophiacodon), to show the general pattern of limb construction in early tetrapods.

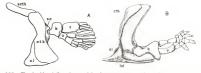


Fig. 132. The shoulder girdle and pectoral fin of a crossopterygian, A, and the same structures in an ancient Gossil amphibian, B, placed in a comparable pose to show the basic similarity in limb pattern. A, r, and u, Huments, radius, and ulm of the tetrapod and obvious homologues in the fish fin. cl. Clavicke; cth, cleithrum; icl., interclavicle; κ, καμριάς κth, supracleithrum. (A after Gregory.)

rangement of distal elements, out of which may have arisen the hand or foot pattern of a tetrapod.

From the first there appear to have been notable differences between the front and hind ilms for tetrapods, as may be seen, for example, in the contrast between the major joints in the two limbs. The forearm rotates freely on the hunerus, but the knee is a simple hinge; on the other hand, the manus cannot be rotated on the forearm, whereas in all tetrapods until the manumals are reached the ankle preserves considerable powers of rotation. These differences can, it seems, be traced back to a contrast in the way in which the two land limbs arose from the fish fins (Fig. 133). It would appear that the pectoral fin gained contact with the ground by a sharp rotation at the elbow which brought the distal part of the limb forward, so that the toes were immediately placed in a proper forward-pointing position. In the hind limb, apparently, the limb was directed straight outward, reaching the ground by a simple flexure at the knee. As a result, the cust would have pointed laterally if there had not occurred further evolution of the ankle region, including rotary potentialities, to enable them to be properly directed forward.

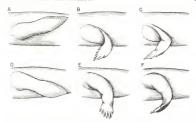


Fig. 1.3. Diagrams to show the postural shift in the paired limbs in the transition from fish to amphibian. A to C, Pectoral limb; D to F, pelvic limb; A, D, fish position; B, E, transitional stage; C, F, amphibian position (cf. text).

Limb Function and Posture. In fishes, as we have noted, propulsion is accomplished by undulatory movements of the body. In land vertebrates with primitive bodily proportions, such as salamanders (Fig. 120, B, p. 148) body undulations appear still to play considerable part in locomotion, with the limbs acting in great measure merely as stationary organs through which the push of body undulations may be exerted on the ground. In tetrapods generally, however, the limbs have taken over a positive and dominant role in progression. In primitive tetrapods, as in urodeles, turtles and lizards today, the limbs were widely sprawled out from the sides of the body, with necessary expenditure of much energy in keeping the body off the ground. Improvements on this situation have been made by numerous tetrapods. In the ancestral ruling reptiles there was a strong trend toward bipedalism, with powerful hind limbs turned forward beneath the body, giving not merely a longer stride but direct support of the body on the vertically placed limbs. With the freeing of the fore limbs from use in terrestrial locomotion followed their development as wings in pterosaurs and birds; on the other hand, many dinosaurs and the crocodilians reverted to a four-footed, quadrupedal, mode of progression. The ancestors of the mammals also improved their gait and gained more effective body support by bringing the limbs into a foreand-aft pose close to the body. Here, however, both front and hind limbs were concerned; the mammals in general are good four-footed runners, although there have been numerous departures from this locomotor pattern, ranging from flying types to marine forms. Reversion to a water existence has been common among tetrapods, and various reptiles, such as certain chelonians and the extinct plesiosaurs and ichthyosaurs, became secondarily marine types with modification of the limbs into flippers (Fig. 134). Still other tetrapods have secondarily reduced or lost their limbs (apodous amphibians, various lizards, snakes) and have reverted to progression by body undulations, essentially "swimming" on the ground or beneath it.

Major Limb Bones (Figs. 135–138). The primitive tetrapod humerus was a stout bone, expanded at both ends. In many later forms it assumes a more

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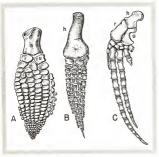


Fig. 13.4. Examples of tetraped appendages retransformed into fishible paddles in marine forms. Pectoral limbs of A, an inthityosaur; B, a plesiosaur; C, a whale. In all there has been a shortening and broadening of the proximal hones amultiplication of the phalanges. h. Humerus; r, radius; u, ulna. (A after Huene: B after Williston; C after Flower, C. after Stone; C. after Flower, and the control of the phalanges of the proximal p

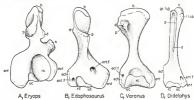


Fig. 135. Humeri of A, a Paleonsie amphibiane, B, a primitive fossil regilie, C, a lizard, D, the opesum, all from the under surface. Primitive humeri were ober, practically witton a shaft, and much sum, all from the under surface. Primitive humeri were ober, practically witton a shaft, and much suppose thin). In all a prominent creat is present to which is attached the pectorials and delaid mucales. In later types the hone became relatively long and slender, particularly in small animals. In primitive regules, forarmian developed distally to the inner or posteries side fentipenophus forames, ear. f.) and on the outer or anterior margin (eccipionolylus foramen, ear. f.). The former forames pressits in various nammals and its Sphendon, the latter in many regilies. A Deloid crest ex-exceptionolyles for attachment of extensor nuscles of forearm; ear, estepicondyle, for attachment of steven suscless of forearm gr. nbb, greater theoretisty, for attachment of supraspiantus and infraspiantus nuscless; headed, lunklesser tuberosity, for attachment of suparaspiantus and infraspiantus nuscless; headed lunk or probles (uppirated) which in replies a sits in formation of exceptionolylus forames, ex, unbut condyles, or proceducompared to the probles of the officiants of exceptionolylus forames, ex, unbut condyles, or procedu-

slender build, but there persist proximal processes for muscular attachment, and there is always some degree of breadth distally, where articular surfaces are present for both radius and ulna and where expansions must be present to furnish areas of origin for the musculature of the forearm. This distally expanded portion

Fig. 136. Radius and ulna, seen from the anterior or extensor surface in A. a primitive reptile, B., a bear, representing a typical mammalism condition; and C., a horse. The humers articulates with the curved surface of the notch in the ulns and the adjacent head of the radius; above, the projecting observation of the ulns serves for the attachment of the powerful triceps muscle, which extends the foreram. In many nammads, as in the horse, the lower part of the ulna is reduced and fused with the radius.





Fig. 137. Femora seen from the ventral surface. A, Primitive fossil amphibian, B, a urodele, C, a primitive regulie. D, a manual-like regulie, E, the horse. The proximal end above; distably, the articular surfaces for the tibia. c, Head (capitulum), int. tr., internal trochaster of primitive forms, for attachment obstructor externus muscle or equivalent, tr. 3, third trochaster of perisosdactyls for part of gluteal muscles; tr. 4, fourth mechanics, to which are attached unit muscles pulling the fenur backward for many amphibians and reptilies, tr. min., lesser (minor) trochaster for illopsoos muscles of mammal; tr. mj., greater (manjor tochaster of mammals, for gluteal muscles).

Fig. 138. The left tibia and fibula, seen from the extensor (dorsal) surface, of A, a primitive reptile of Permian pelyossurf with a fibula of good size, B, the pig. showing a primitive mammalian condition, with the fibula complete, although slender; C the horse, exemplifying a type with reduced fibula. cn, Cnemial crest.



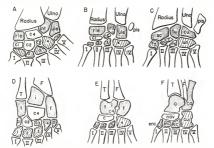
is frequently pierced by foramina for nerves to the lower part of the limh, and one of these, on the posterior (or inner) margin is frequently preserved in mamls. The columnar radius is the main supporting element of the forearm. The shaft of the ulna bears little weight, and the bone tends to be slender and in many mammals fuses with the radius. The head of the bone—the olecranon or "funny bone"—projects above the notch for articulation with the humerus and is important as the point of attachment for the main muscle which extends the forearm.

The femur in primitive forms was essentially a stout rodike structure, with proximal processes—trochanters—for muscle attachment, but, in contrast with the humerus, the bone is not greatly expanded either proximally or distally. In primitive forms the femur projected nearly straight out laterally from the acetabulum, and the articular surface for the girdle lay, in consequence, directly on the head of the bone. But in some reptiles, and in all mammals, where the limb is rotated to a forward position parallel to the main axis of the body, the head is of necessity turned inward at more or less a right angle to the shaft.

In the lower leg or "shin" segment, the inner bone, the tibla, like the radius in the front leg, is the main weight-bearing element, and the fibula, on the outer side, is (like the ulna) more sleader and mainly serves as an area of origin for musculature. These two hones are, however, quite unlike their forearm counterparts in appearance. The head of the tibia is expanded in triangular fashion to underly most of the distal end of the femur. The fibula, unlike the ulna, has no proximal projection, and the main extensor muscle of the thigh attaches instead to a prominent crest on the tibia.

Feet (Figs. 139–146). The proximal part of the manus, or hand, consists of a series of small elements, the carpus, forming a flexible adjustment between the arm and the digits. In a primitive tetrapod this consists of a dozen hones—three proximal hones termed radiale, intermedium and ultrare, four centralia and we distal carpals, one for each toe; in reptiles there is added a pissform on the radial side. The history of these elements in the various classes is a complex and variable one which cannot be followed in detail in any limited space; numerous variants are to be seen in the figures. In general, there tends to be considerable reduction or fusion of elements—particularly loss of centralia, of which few forms retain more than one or two, and of the fifth distal carpal, an enlarged fourth element generally supporting the two outer digits. The carpal elements of a mammal are readily identifiable in terms of the primitive arrangement, but (regretably) special names—in fact, at least two sets of such names—have been applied to the carpal bones. One such mammalian series is shown in Figure 130. C.

Beyond the carpus lie the toes, or digits. In each a proximal joint lying in the flesh of the palm is termed a metacorpal; the distal joints are the phalanges. The presence of five digits appears to have been a primitive condition, and except in the "flipper" of some lossil ichthyosaurs is never exceeded. On the other hand, reduction is common. No modern amphibian has more than four digits in the hand; dinosaurs and their kin tended to reduce the number by loss of the outer digits, and birds have remains of only the three inner fingers in the wing skeleton. In primitive mammals the first toe tended to be set off from the others as an aid in grasping—the thumb or pollex; this is reduced in many running forms. In the hoofed mammals, the ungulates, there is frequently further loss. In



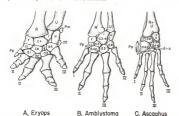


Fig. 140. The left mamus of amphibians, including an early labyrinthodout, a undele, and an anuran. Restured elements in d in broken line. All twelve elements thought to have been present in the principle carpus are lound in Expoys, in modern amphibians intoins on various such have occurred. An in most amphibians, four toes are present in the forms figured, although all have some development of a digit medial to be pollex, and an element in Expops may have been the study of an extra toe beyond reduced fith digit. The phalingard count of two or three is usual in amphibians, of to of, Centralia; c. pais-curieform; d-la, Sidiani carpals, it intermedium, I, lunare, on, magnum at 1, 35, metacarpals; positorm; Pm, postuminimum digit Pp, prepollex, R, radius r, radialex, scaphoid; dl. trapeziolic ton, trapezioni, C. otta, a Junice sa, uncidente II b V, digits, (Alfor Cropery, Miner, and Noble)

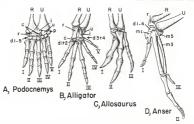


Fig. 141. The manus in A, a turtle; B, the alligator; C, a carnivorous dinosaur; D, the goose. Abbreviatious as in Figure 140. The bird manus includes the fused elements of the first three digits only; a somewhat comparable structure is seen in certain dinosaurs. (A after Williston; C after Gilmore; D after Seiner.)

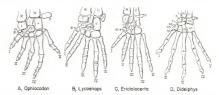


Fig. 142. Evolution of the mammalian manus. A, Primitive reptile; B, a primitive therapsid; C, an advanced therapsid; D, a primitive mammal, the opossum, Abbreviations as in Figure 140. In the carpus there is a loss of the fifth distal element, a reduction from two centralia to one; distally, "supernumerary" phalanges are lost from digits III and IV. (B after Broom; C after Watson.)

the even-toed ungulates—the artiodactyls—digits II and V are reduced and may be lost, leaving toes III and IV to form the "flowen" hoof of a cow or deer. In odd-toed ungulates toe V as well as the pollex was early lost, giving a three-toed foot, and in modern horses only the central digit—toe III—remains. In ungulates toe reduction is usually paralleled by an elongation of the metacarpals, which has the effect of adding a third major segment to the limb and a correlated increase in speed.

A phalangeal formulae gives in brief form the count of phalanges in each digit from the first toe outward. The number of joints present in primitive terapod toes is uncertain; in amphibians there are seldom more than three. In primitive reptiles, however, there was set up a formula of 2.3.4.5.3, and this count is maintained in a variety of reptiles, notably the lizards. In the transition from reptiles to mammals there tended to be an "evening up" of the toes and the development of the formula of 2.3.3.3.3. This is still the digital count common in primates (such as man); in mammals in which the number of toes is reduced, those present generally retain the typical number of joints. Very seldom in amniotes is there any secondary increase in the number of phalanges in a toe, the only exceptions being in the "flipper" of such aquatic forms as the extinct ichthyosaurs and plesiosaurs and the whales.

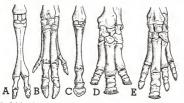


Fig. 1.83. Left front feet of ungulates—in order, camel, pig, horse, rhinoceros, and tapir. The first two are artiodactyls, in which the axis of symmetry lies between the third and four toes. In the pig (B) lateral toes, 2 and 5, are complete but small. In most artiodactyls, as in the camel (4), the two man metapodials are fused into a canson hone. The three remaining forms are perisonductyls, in which the axis runs through the third lote. In the tapir (E) the policy is lost, but the other four toes remain; in modern thinoceroses (B) the fifth toe has disappeared; in modern horses (C) the second and fourth are reduced to splints. (After Flower,)

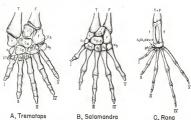


Fig. 144. The pes of amphibians, including A. an early labyrinthodout, B. a salamander, and G. a frog. The tursus of Trenatops includes all elements presumed to be present in ancestral hetrapods, as well as an additional pretursal bone. In the unded some intuition of tursal elements has occurred frog, thiale and fibulare are so elongated as to constitute an additional limb segment; except for a few small distal elements, the face of the other tursal bone is not clear. Five too are typically present so contrasted with four in the manns, and the count of phalanges is generally higher in the pes than in the amphibian manns of Fig. 140). The frog has a developed prehallux, I so, Centraliz, all to diff, disultances of the contrast of the contr

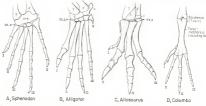


Fig. 145. The pss in repitles and brids. 4, Sphenodous ft, the alligator, C., a carnivoress dimonstructure. D. the pignon. In all forms there have been various types of reduction and fusion of the turnal elements and a trend toward the development of a main joint within the tarson between proximal and discal domests. In the brids all the transits are fixed with the thile proximally or with the funct mentarised distulty, In archosaure, such as the alligator and dimosaure, there is a strong trend toward the loss of the tilly. In archosaure, such as the alligator and dimosaure, there is a strong trend toward the loss of the fifth toe, and it has dispepared in the dimosaur figured and in the brid. Except for the lack of fusion of the mediatrask, the Allosaurus foot is quite similar to that of brids. a. Astragalase, c. calcaneum; other abbreviations as in Figure 144, if the Williston, C. der Glimore.

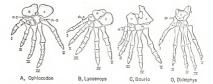


Fig. 146. Evolution of the mammalian type of yea. A, Primitive reptile (of the early Perminn); B, a primitive therapsid (of the late Permian); C, an advanced Triassi an annual-like reptile. B, the opossum, Principal changes include development of a pulley surface on the mammalian astragatus, development of a heel on the calcancum (in C and D), loss of two small tarsal elements, and reduction in phalangeal count (a transitional stage in B). a Astragatus, c calcancum; c lot cδ, centraliz, ck, cubried (in distal tarsals; ec, external cumeiform; ic, internal cumeiform; mc, middle cunciform: ph, prehallux (exceptional in nammals). (B and cafter Schenfler.)

The structure of the tarsus, or ankle region, in primitive tetrapods was very similar to that of the carpus. Twelve elements were present here as in the case of the wrist. There were three proximal elements—tibiale, intermediam and fibulare; four centralia; five distal tarsuls. As in the case of the manus, the centralia tended to be reduced in numbers and the last distal tarsal lost. More striking, however, is a marked change in the proximal region in all ammiotes. The fibulare persists, but on the inner side of the ankle the reduced tibiale fuses with the intermedium and a centrale to form a large bone on which the tibia moves freely. This compound bone is usually called by its mammalian name of astragalus, and the fibulare, its lateral companion, is generally termed the calcaneam, as in mammals. This proximal modification is apparently associated with the need, noted earlier, for rotating the hind foot forward on the shin to bring it into a proper forward pointing position. A further change in the tarsus is the development in mammals of a projecting "heel" on the calcaneam. As noted in Chapter 9 this is associated with the development here of an attachment of the major calf muscle through the "lendon of Achilles."

The build of the toes of the hind foot is very similar to that of the fore foot, the proximal joints, however, are (naturally) termed metatarsals rather than meta-carpals. Five digits in the pes appears to be the primitive number, and this number is retained in most amphibians and reptiles. In dinosaurs and birds there was a trend toward the development of a foot with three toes, digits II—IV pointing forward, the center one the longest; the first toe is reduced or turned backward as a prop or aid in perching. In mammals the first digit of the foot—the hallux—early became specialized as a grasping structure. Digital reduction in the pes of fast running mammals paralleled that seen in the "hand," with general loss of the pollex and, in many forms, further reduction to a two-toed condition in artiodactives and a monoadcavit condition in horses.

As in the manus, amphibians tend to have but few phalanges per digit in the foot, but in early reptiles there appeared a phalangeal formulo of 23.4.5.4, almost identical with that of the hand. This count was retained in most reptilian groups (although many turtles tend to some reduction in both fore and hind feed). We noted, above, the symmetric build of the toes in many dimosaurs and in birds. It is of interest that this symmetry has been attained without modification of phalangeal numbers, for the long third toe has commonly 4 phalanges, and the two shorter ones, inner and outer, have 3 and 5 joints respectively. Mammals have reduced the phalangeal count in the pes, as in the manus, to 2.3.3.3.3. Again as in the hand, the phalangeal count tends to be persistently constant under conditions of toe reduction. Only in aquatic reptiles—again as in the manus—is there any increase in the number of phalanges in a given digit of the pes.

#### VISCERAL SKELETON

Between the gill openings of water-breathing vertebrates lie cartilaginous or bony hars which are the basic components of a set of structures termed the visceral skeleton. The visceral elements form but a modest part of the skeleton, but they are versatile structures in their potentialities. Primitively this entire series acted as gill supports, but early in vertebrate history anterior visceral arches were transformed into jaw bars; and although gills have disappeared in amniotes, persistently surviving visceral elements are to be found, even in mammals, in such varied areas as the skull, auditory ossieles and laryux.

We shall note elsewhere that the gill region is unique in its musculature and nerve supply; its skeletal elements are unique, also, particularly as regards their embryologic origin. Like other cartilages, those of the visceral system are derived from mesenchyme; but this mesenchyme, most exceptionally, is not of mesodermal origin—it is, instead, derived from the ectoderm. We have noted in our embryologic review the development of the neural crest. The main derivatives of this structure are elements of the nervous system. In the head region, however, neural crest cells migrate downward and form a mesenchyme material 172 THE VERTEBRATE BODY

from which the gill arch system (and in addition a fraction of the braincase) is formed

The Gill Skeleton. In cyclostomes (Figs. 106, p. 140; 147, A) part of the gill skeleton is specialized to form the supports of the peculiar rasping "tongue." The remainder forms a lattice-work surrounding the gill pouches. Whether or not this is a primitive condition is uncertain; but in all more advanced fishes, at any rate, the gill supports consists (except for cases of secondary fusion) of a number of series of jointed bars, following one another in sequence along the walls of the pharynx between successive gill slits. These visceral arches are serially arranged, as are the gill openings, but this serial arrangement is not, apparently, related to the segmentation seen in other parts of the body, which is founded on segmentation of the mesodermal somites. Each typical gill arch of a jawed fish (Figs. 147, C, 148, 4; 190, p. 217) includes on either side a major dorsal element, an epibranchial, and a major ventral one, a cerato-

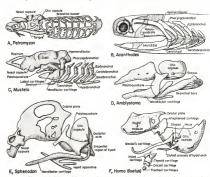


Fig. 147. Visceral skeletou and braincase in representatives of six vertebrate classes; 4 to C, adult forms, D to F, embryos, cartillage singled, hose unstippled, A. The lampsev, with a peculiar braincase and associated cartilages not readily comparable to those of other groups; the branchial backet is fund antiroidy to the horizones. B, Polocose; piny' "shart," a placoderum in which joss are developed, but here below the manufalled. C, Shark, with hysotylic jav suspension. D, Salamander, the pullroquisation is reduced, and the branchial actors are reduced even in the embryo of larce. F. The replicit Sphero-don. The braincase is incompletely formed (cf. lizard in Fig. 117, D), and hyoid and hranchial lars are reduced to a hyoid apparatus and stapedial cartillage, F, Human facts. The replicit Sphero-don. The braincase develops only ventrally and anteriorly around the brain. The pulstoquadrate is reduced to a hybor group and the brain. The pulstoquadrate is reduced to a high enough and most group and the pulstoquadrate is produced to a hybor group and the pulstoquadrate is reduced to dispheroid and most expandent, The lower jaw (Meckel's arthlige) is reduced, he proximal part becoming the mulleus in the cartilages, (A and C after: Goodwich; B after Waston; D after Horstadius and S-limm; E after Hoves and Svinnerum, F after Guapp, Mackley

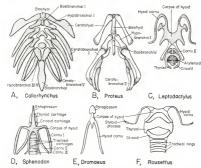


Fig. 148. Gill hars and tetrapod derivatives, in ventral view, in A, a chimaera; B, a water-dwelling salamander; C, a frog; D, a reptile, Sphenodon; E, the cassowary; and F, a bat. In A the doresil arch elements are not included. In C, D, and F laryngeal cartilages are included. The entoglossum of D and paraglossum of E are tongue-supporting anterior developments from the body of the hvoid.

branchial. There is frequently a pharyngobranchial at the top of the arch and a short hypobranchial below the major ventral element. Ventrally, median structures—basibranchials or copulae—tie the arches of the two sides to one another and connect successive arches. The gill bars generally bear a row of short gill rakers on their inner margins, and gill rays which extend outward and stiffen the gills (Fig. 227, p. 245). In most jawed fishes five typical arches are present.

Jac Development. The development of jaws was one of the greatest advances in vertebrate history—one which brought about a revolution in feeding habits and mode of life. The visceral arches played a leading role in this process, for a pair of transformed gill arches are basic structures in jaw formation. Indeed, they form the entire jaw structure in sharklike fishes. It appears that with the development of an expanding mouth cavity, a pair of gill bars lying adjacent to it enlarged; the epibranchial element of this arch became the palatoquadrate cartilage forming the shark upper jaw; the corresponding ceratobranchial became the mandibular cartilage of the lower jaw (Figs. 147, B, 149). Various lines of evidence suggest that the jaws are not the most anterior of the original gill arch series, but that one and probably two sets of anterior bars were crowded out of existence as the mouth expanded.

In bony fishes and tetrapods, dermal elements play a major part in jaw formation, and the role of the gill arch cartilages or the bones that replace them is much reduced. However, at least that part of the primitive cartilages which forms the articulation between upper and lower jaws persists as high up the scale as reptiles and birds, and relics of these elements persist even in mammals, although, as will be seen, in curiously modified form.

Jaw Suspension. It is believed that in the ancestral fishes the jaws articulated with the braincase without additional support—the autostylic condition. This articulation was primitively by movable joints, but in some fishes-chimaeras and lungfishes-there is a firm fusion of the upper jaw cartilages with the braincase. Forms in which autostyly is present are, however, the exception in fishes, for the next set of gill bars behind the jaws, termed the hvoid arch, generally are called in to aid in suspension of the jaws on the braincase. The major ventral element of this arch, the ceratohyal, is little specialized; however, the main dorsal element, the hyomandibular, becomes a stout bar which dorsally is braced against the otic region of the braincase and ventrally is tightly bound by ligaments to the region of the jaw joint (Fig. 149, C, 150). In a few sharks the jaw is supported both by the hyomandibular and by a direct connection of jaw and braincase-the amphistylic condition. In most sharks and bony fishes, however, the upper jaw loses any major direct connection with the braincase and the jaws are propped solely by the hyomandibular; this mode of support is termed hyostylic. In land vertebrates the hyomandibular no longer acts as a jaw support; upper jaws and palatal structures form their own connections with the braincase and skull roof shield, and hence are autostylic in construction.



Fig. 149. Diagrams to show evolution of jiss and byoid region. Gill openings in black. H. Hyromadiblubur S, spiratoral gill site. In A, a primitive justees condition. B, lass formed from a pair of gill arches (two anterior arches and sits may have been lost in the process); spiracular gill sit unreduced, and byomandiblut not specialized. This condition may have preciseled in the extinct placederms. C. Condition seen in most jaced fashes; the hyomandibular has become a jac support, and the intervening till sit reduced to a suitarle.

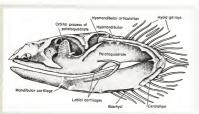


Fig. 150. The cranial skeleton of a shark, Chlamydoselache: braincase, jaws, hyoid arch. (After Allis.)

Tetrapod Gill Arch Derivatives (Figs. 147, D-F; 148, C-F). Except in larval amphibians the gills have lost their function in the tetrapod classes and in correlation with this the gill bars are reduced and modified in structure. The history of the elements associated with the jaws and that of the hyomandibular (which becomes an auditory ossicle) is discussed elsewhere. The remainder of the old gill bar system becomes associated with two structures prominent in tetrapods but little developed in fish groups—the tongue and the lung apparatus for breathing.

The main body of the tongue is a mass of muscle; embedded in its base, and extending from it backward and upward around the sides of the pharynx is the hvoid apparatus. The main body of this structure-the corpus-is formed from one or more of the median ventral arch elements present in the fish, Expanding outward and upward from the corpus are slender "horns"-cornuawhich represent the main ventral elements of the hyoid and succeeding gill bars of the ancestral fishes; sometimes small dorsal elements are appended to the horn tips. Three such pairs of "horns" are frequently present in amphibians and reptiles; two pairs in mammals; a single pair in birds.

The windpipe, leading to the lungs, is supported in land vertebrates by cartilages which are modified parts of the visceral arch system. Just beyond the entrance to the windpipe there typically develops an enlargement of the tube, the larynx (cf. Chap. 11). The basal part of the hyoid apparatus generally lies close to the front end of the floor of this cavity, but in addition a series of special cartilages tend to form a complex laryngeal skeleton around it. In most tetrapods the windpipe, the trachea, is strengthened by ring-shaped tracheal cartilages. which are not directly comparable to any specific fish elements but are reasonably to be regarded as new developments of the visceral skeletal system.

## 8

### THE SKULL

The term "skull" is used in somewhat variable fashion. In a broad way it refers to any type of skeletal structure found in the head region. In this sense one may consider the lamprey or shark as having a skull composed of a braincase and other isolated cardiages. But in common parance the term has a somewhat different meaning. The familiar skull of every form from a bony fish to a mammal is a fused unit structure, in which braincase and upper jaws are welded together by a series of dermal bones; the lower jaw is not included.

In the old ostracoderms and placoderms there appears to have been some sort of fused head skeleton forming a skull in this sense, but in most of these older fishes the structure is too aberrant and too incompletely known to be considered here. In higher bony fishes and all tetrapods there is a well-constructed skull, with many common features throughout. Even so, it is difficult to give a generalized description based on any one living type, for most have become so specialized or degenerate that the true phylogenetic story is obscured.

But in the case of the skeleton, in contrast with other organ systems, we have the advantage that in many instances there are preserved as fossils the bones of actual forebears. We have a fairly complete knowledge of the head structures of the ancient labyrinthodont amphibians of the late Paleozoic, whose skulls are of the very type from which those of all later tetrapods have been derived. Further, this type is not far removed from that of the crossopterygian fishes from which land forms have descended, and through them this ancestral tetrapod skull pattern can be "tied in" with that of other bony fishes. We shall, therefore, give at this point a fairly full account of this central skull pattern and then discuss the major modifications seen in the various fish and tetrapod groups.

Skull Components. To avoid (as far as possible) mental indigestion in the description of this complex structure, it is best that it be resolved into components (Figs. 151, 152). The skull includes both dermal bones and cartilages, or their bony replacements, of both somatic and visceral nature (cf. p. 131). One possible method of treatment would be to consider as units the elements derived from each of these three embryologic sources. It is, however, preferable to recognize that a primitive skull seems to be composed of three major functional units, one purely dermal, the other two composites, as follows:

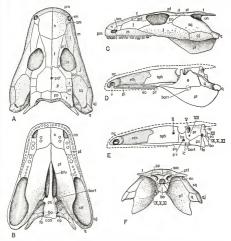


Fig. 151. The skull of an ancestral land vertebrate, based primarily on the Carboniferous labyrinthodont, Plaheogyrimus. A Dorant view of dermal skull roof, B, palate, C, lateral view; B, lateral view with dermal skull roof removed (outline in broken linie); palatil bones—dermal and endoskeletal—oll eft side are shown; deep to them, the braincase. The hatched area is the sutural surface of palatal bones against mutilla. E, Lateral view of braincase, F, posterior view, Graffyr after Watson.

A. A dermal shall roof—a shield of membrane bone covering thoroughly the top and sides of the head and extending down to the jaw rims, where the shield elements bear the marginal teeth. The roof is unbroken save for openings for the nostrils (external nares), eyes (orbits), and a small parietal foramen for a third, median eye. On either said the shield is notched behind the orbit in early

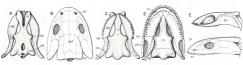
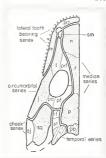


Fig. 152. Diagram to show the components of the skull. A, C, E, Dorsal, ventral, and larent views of endosticelal structures of brainness and palate (or upper just) as present in a shark or an embry of the just of the order of the contractive of the property of the contractive of the contra

tetrapods for the eardrum opening, which replaces the spiracle present here in bony fishes.

- B. A palatal complex. This includes ossifications in a palatoquadrate cartilage of visceral origin (which in sharks forms the entire upper jaw), and in addition a series of membrane bones formed below this cartilage in the roof of the
  mouth and in great measure replacing it. The anterior portion of this complex
  forms a broad palatal plate with, anteriorly, lateral gaps for the internal nares, or
  choanae. Posteriorly the palatal complex on either side is separated from the edge
  of the shield by the subtemporal fossae, through which descend the temporal muscles for closing the jaws.
- C. The braincase, formed in cartilage (mainly of somatic endochondral origin) but usually ossified to a considerable degree; to its lower surface, in early tetrapods and bony fishes, is applied a sheet of dermal bone formed in the central area of the mouth vault.
- The Primitive Amphibian Skull. Dermal Root. In a primitive tetrapod the dermal skull roof includes a considerable number of elements, mainly paired, which are suturally united to form a practically solid armor. Some of these elements are lost in variable fashion in later tetrapods; many, however, are important in every group of bony vertebrates. It is a strain to commit to memory this series of names. As an aid we may arbitrarily group them in several series (Fig. 153):
- (a) Tooth-bearing marginal bones, the small, anteriorly placed premaxilla and the large maxilla.
- (b) Paired elements along the dorsal midline, including nasals, frontals, parietals and postparietals. Except for the last, these are always prominent skull elements.
- (c) A circumorbital series of five bones—prefrontal, postfrontal, postorbital, jugal and lacrimal. Only the last two persist to the mammalian stage. The lacrimal carries a canal for the tear duct, (We may mention here a small and varieshed bone tucked into the nasal cavity which does not fit well into any series—the sentomaxilla.

Fig. 153. A diagram of the skull roof of a primitive tetrapol with the elements grouped (rather arbitrarily) into regional series. (The little spranger arbitrarily) into regional series. (The little spranger are really fit into any series.) The support to be fused into the mammalian occipital bone. The proper to be fused into the mammalian occipital bone. Fromtal & interremponal & pigale, bearinal, maxillar, a nasal; p. partents pf. promotion promovaling propermitality por premarkillar positional properminal portion of the promotion of the prom



(d) A temporal series forming a fore-and-aft row above the otic notch and behind the orbit. These small bones—intertemporal, supratemporal, tabular tend to be reduced or lost in most tetrapods.

(e) Cheek bones; the squamosal, a large and persistent element, and the quadratojugal.

Primitive amphibian skulls frequently exhibit grooves on the skull roof (and on the outer surface of the lower jaws) in which lay the lateral line canals. In bony fishes these canals are usually sunken within the bones, with pores opening to the surface.

PALATAL COMPLEX (Fig. 151, B, D). This includes bones formed in the palatoquadrate cartilage, which here forms part of the palate (rather than an upper jaw). In tetrapods there are two such elements. The epipterygoid articulates at its base with the braincase (movably so in fishes and many early amphibians and some repiles) and extends upward toward the skull roof. Behind this is the quadrate, which persistently forms the lower jaw articulation in all classes except mammals.

Much more prominent, however, in this complex are dermal bones formed in the roof of the mouth which in great measure supplant the cartilage and its ossifications. The major element is the pterygoid, which extends much of the length of the skull. This is bordered anteriorly and laterally by three smaller bones romer, palatine and ectopter goid (the last reduced or absent in many later terapods). The anterior part of the complex forms on either side a pair of essentially borizontal palatal plates, separated by interpterygoid vacuities of variable proportions. Behind the point of articulation with the braincase this plate ends; posteriorly there is a vertical plate, formed by pterygoid and quadrate, which swings back and out to the jaw articulation, medial to the subtemporal fossa.

The Braincase (Fig. 151, B, E, F). In most groups of bony vertebrates a median dermal element, the parasphenoid, is closely applied to the under surface 180 THE VERTEBRATE BODY

of the braincase; it is often difficult to distinguish it from the braincase proper (and in mammals and birds it has ceased to exist as a separate element). The braincase itself is generally well ossified, but the region of the nasal capsule never ossifies in typical land forms, and in modern amphibians braincase ossification is much reduced. In well ossified forms the bony elements of the braincase frequently fuse in the adult, making interpretation of the individual bones difficult.

The occiput includes a ring of four bones—the paired exoccipitals on either side of the foramen magnum, and the median supraoccipital and basioccipital above and below; the condyle (primitively single) is carried by exoccipitals as well as the basioccipital. The hypoglossal nerve (XII), except where lost in degenerate modern amphibians, pierces the exoccipital, the vagus complex (X and XI) and a vein usually emerge through a foramen (jugular) just in front of the exoccipital, and nerve IX has its exit here or by a separate opening just ahead of this point. On either side, in front of the occipital bones, is the region of the otic capsule containing the internal ear. In primitive land vertebrates this ossifics as two elements, promic and opisthoric, and in tetrapods there is present an external opening, the fenerata oralis, into which fits the base of the sound-transmitting stapes (evolved from the fish hyomandibular). Nerve VIII, of course, enters the inner surface of the capsule, enerve II penetrates to the outer surface of the braincase by a canal in the prootic, and nerve V emerges through one or more openings at the anterior magnetin of that bone.

Forward from the otic region the braincase rapidly contracts in width to the sphenoid region lying between the orbits. A major element here is the basisphenoid, a median ventral ossification, sheathed below by the parasphenoid. It contains a pocket (or fossa) for the pituitary (not seen in the figures) and laterally sends out a basal process for articulation with the palatal complex. Ventrally the internal carotid arteries pierce the bone to enter the brain cavity; the side walls are variably developed but contain at least a major opening for the optic nerve (II) and allow emergence of the small eye muscle nerves (III, IV, VI). The anterior end of the primitive tetrapod braincase, as far as ossified, is formed by a single large median element, the sphenethmoid, which is still present in rather primitive fashion in the living anurans. This contains the olfactory nerves, running back from the cartilagionus nasal capsules.

The Skull in Bony Fishes. Having seen the general plan of a vertebrate skull in a representative and rather primitive type, we may now proceed to study variations on the "theme" which it presents, beginning with a comparison of its structure with that of bony fishes. Logically we should begin with the crossopterygians (now quite extinct except for one specialized form), since they include the ancestors of land vertebrates. In these forms (Fig. 154) most major elements of the skull roof and palate can be readily identified in terms of tetrapod bones. They differ, however, in certain regards; in front, the nasal and "rostral" region include a rather variable mosaic of small bones (probably a primitive condition), and posteriorly there is an extra row of "extrascapular" bones which are not part of the skull proper. Notable, however, are differences in proportions; the crossopterygian has a very short facial region in front of the orbits and a long postorbital length, so that the posterior bones of the roof are much elongated. The braincase of the ancient crossopterygians was highly ossified—so completely so that sutures are obscured and individual elements cannot be made out. In many features the braincase (Fig. 154, D), too, is like that of a typical early amphib-

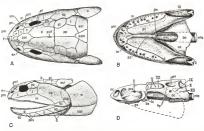


Fig. 154. The skull of a Paleozoic crossopterygian (composite), for comparison with that of a primitive land vertebrate (cf. Fig. 151). A. Dorsal view, B. palatal view, C. lateral view, D. lateral view of braincase. From the crossopterygian dermal covering that of a labyrinthodont differs primarily in loss of opercular elements and posterior row of hones on roof; relative reduction of length of posterior part of skull and elongation of "face" region; reduction of small elements in rostral and nasal region. The palate is similar in the two. The labyrinthodont braincase is less completely ossified, formed in one piece instead of the two present in crossopterygians, and lacks the greatly expanded notochord of the latter, a. angular; bo, basioccipital; bs, basisphenoid; d, dentary; ec, ectopterygoid; en, external naris; esl, esm, lateral and medial extrascapulars; f, frontal; g, gulars; hy, hyomandibular articulation; ic, foramen for internal carotid; in, internal naris; it, intertemporal; j, jugal; l, lacrimal; m, maxilla; n, nasal; nc, nasal capsule; ntc, notochord (restored); o, opercular; oc, otic capsule; p, parietal; paf, parietal foramen; pf, postfrontal; pl, palatine; pm, premaxilla; pn, postnasal; po, postorbital; pop, preopercular; por, postrostral; pos, postsplenial; pp, postparietal; prf, prefrontal; prs, presphenoid (sphenethmoid); ps, parasphenoid; pt, pterygoid; ptf, posttemporal fenestra; q, quadrate; qj, quadratojugal; r, rostrals; sa, surangular, sm, septomaxilla; sop, subopercular; sp, splenial; sq, squamosal; st, supratemporal; stf, subtemporal fossa; t, tabular; v. vomer. Roman numerals, foramina for cranial nerves. (A and B based on Eusthenopteron; C based on Osteolopis; D based on Ectosteorhachis; data from Jarvik, Romer, Säve-Söderberg, Stensiö.)

ian. There is, however, one seemingly major stumbling block in the comparison of braincases in the types—a stumbling block which at one time led to the belief that crossopterygians were too specialized to be ancestors of the tetrapods. The braincase is formed in two discrete pieces, front and back, which can move in somewhat flexible fashion; and the hind half is perforated by a great ventral tunnel for an enormous notochord. These unusual structural features are not found in ordinary tetrapods, even in amphibians as primitive as that here used as a type, and it was long felt that the crossopterygians were specialized in braincase build. Very recently, however, there have been found braincases of the very oldest amphibians from the late Devonian. In them (to our astonishment and delight) there is seen a large notochordal canal, and while there does not appear to have been motility between braincase halves, there is distinct evidence of its ossification in two units. Thus, here (as in many other instances) structures once thought to be "aberrant" or "specialized" in actuality represent ancestral conditions.

The dipnoans are related to crossopterygians (and hence to tetrapod ancestors); but in their skull structures (Fig. 155) they have branched off in an entirely independent direction; they need be described only briefly. The roof has lost much of its original extent (particularly in the living genera) and is repre182 THE VERTEBRATE BODY

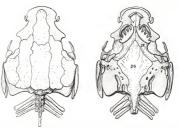


Fig. 155. Skull roof and palate of the Australian langish, Epiceratodus. The braincase (stippled) is cardiaginous, but is underlain by a large parasphened (op); the derman for oil nucleas only a small series of large plates which cannot be readily homologized with those of other forms. The upper pass are fund to the braincase, and the only omiscinson in the upper jaw to palate are large pareygoids (pd) and vone (vi). Large fan shaped toothplates are borne by the pterygoids, and a small enting toods in present on each voner. (Atter Goodrich).

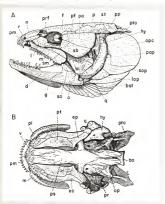


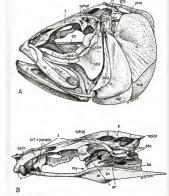
Fig. 156. A, Lateral and B, palatal views of Amia, least specialized of living actinopterygians. Abbreviations: a, angular; bo, basioccipital; bst, branchiostegal rays; d, dentary; ec, ectopterygoid; ep. epipterygoid; f, frontal; g. gular; hy. hyomandibular; iop, interopercular; l, lacrimal; m. maxilla; n. nasal; op, opisthotic; opc, opercular; p, parietal; pf, postfrontal; pl, palatine; pm, premaxilla; po, postorbital; pop, preopercular; pp, postparietal; pr, prootic; prf, prefrontal; ps, parasphe noid; pt, pterygoid; pto, pterotic; q, quadrate; r, rostral; sa, surangular; sb, suborbital; sm, supramaxillary; sop, subopercular; st, supratemporal; r, vomer. (The identity of certain of these elements with similarly named bones in crossopterygians and tetrapods is uncertain.) (After Goodrich.)

sented by variable plates which cannot be readily identified. Most of the bones of the palate (except for large pterygoids) have been lost or remain as cartilages; the braincase has many features comparable to those of a tetrapod, but remains purely cartilaginous in the modern lungfishes and even in most fossil genera. In the skull as in the rest of the body the lungfish skeleton is thus highly degenerate.

The rav-finned fishes (except for the sturgeons and paddlefshes) have a well-ossified skull (Figs. 156, 157) which is comparable as to main components and their arrangement with that of early tetrapods and crossopterygians (although the braincase is never as completely subdivided as in the latter group). When, however, we try to compare and name individual bones, we are in grave trouble. It is probable that the actinopterygians diverged at an exceedingly early date from the line leading to the crossopterygians and their tetrapod descendants and that in consequence their bone patterns have little relation to those seen in the other group. Most living actinopterygians are teleosts, in which, among other specializations, there is great reduction of the check region, a shortening of the jaw gape, and a loosening and reduction of the upper jaw elements.

History of the Tetrapod Skull Roof. Rather than discuss seriatim the changes rung on the primitive tetrapod skull pattern as a whole, in group after

Fig. 157. The teleost Clupea (herring). A, Lateral view of skeleton of head and gill cover; B, lateral view of braincase. The structure of teleost skulls is highly specialized, but derived from the general pattern seen in Amia. Abbreviations: ar, articular, bo. basioccipital; d, dentary; deth, dermethmoid; dsph, dermosphenotic; epiot, epiotic; f, frontal; hyom, hyomandibular; iop, interopercular; L lacrimal; m, maxilla; my, opening of myodome (arrow); n, nasal; o, opercular; orbsp, orbitosphenoid; p, parietal; pareth, parethmoid; pm, premaxilla; pop, preopercular; pr. prootic; prf, prefrontal; ps, parasphenoid; ptm, posttemporal; pto, pterotic; q, quadrate; sb 1-5, suborbitals; smx 1, 2, supramaxilla; sop, subopercular; sphot, sphenotic; v, vomer. (After Gregory.)

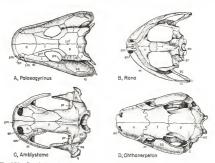


group of higher vertebrates, we shall follow through separately the history of the three major skull components.

In the skull roof, later history is almost exclusively one of loss and degeneration. Almost never is there any development of a new element; always there is, in time, a greater or lesser degree of reduction. No living tetrapod has retained in full the pattern of its early ancestors, and few have preserved a solid roof covering.

Modern amphibians (Fig. 158, B-D) show an even greater reduction of the roof than do most higher classes. In the frogs the roof is reduced to a mere frame of bone outlining the borders of the originally solid roof, there remain but five of some seventeen original pairs of roofing bones—these being premaxillae, maxillae, squamoasls, nasals and fused frontals (with which the parietals are fused). The salamanders present a broader roof, but the reduction in numbers of elements is about as extreme, and the same holds true of the Apoda, in which, however, the elements remaining are fused into a comparab turnoving organ.

In stem reptiles (Figs. 159, A. 160, A) there was little loss of the original pattern of elements, except that reduction of the small hones of the temporal series had begun (and these little elements and the postparietals disappear completely in most reptile groups). In later reptiles (Figs. 159, B. D. 160 B-P) there are numerous and varied modifications in the roof pattern. To some extent losses of elements occur, but major modifications are mainly associated with the development of openings in the check region of the skull—the temporal fenestrate, which offer valuable clues to reptile classification and relationship (Fig. 161). These openings, which afford release to the temporal muscles during their con-



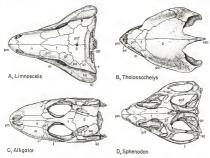


Fig. 159. Donal views of reptilian skulls. A, Stem reptile of the Paleonoic; B, a sea turtle; C, a young alligator. D. Sphenodon. Abbreviations: en, external naris; f, frontal; j, jugal, l, laerimal; m, maxilla, m, anasal; p, parietal; peri, parietal foramer, pf, postfortials, pe, prematile, po, postfortials; pg, poptaprietal; pr, protoc; prf, prefrontal; qj, quadratojugal; soc, supraeccipital; sq. squamosal; st. supratemporal; t, tabular.

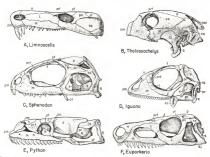


Fig. 160. Side views of repúlian skulls A, Stem regulie of the Paleomics, B, a sea turtle, C. Sphemon, D. al laural, E. a probuse, F, a prime, F, a primitive ruling regulie of a type from which hirds, discossess, and croccolilans have descended. Abbreviations e, epiptersysid; ec, estoptersysid; f, frontalt, j, jugal, t, lackramin, L, latersophenoid, an auxilia; en, assale, p, particle, βρ postformath, μp, permaxilla, p, no expensive tile, pc, province; pf, performat, pc, percynoid, pc, quadrate, gi, quadrate, quadrate, quadrate, quadrate, quadrate, qua

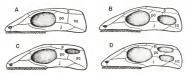


Fig. 161. Diagrams to show types of temporal openings in reptiles. A. Anapsid type (stem reptiles, turtles); B. synapsid type (mammal-like reptiles); C. parapsid type (extinct plesiosaurs, and so forth); D. diapsid type; rhynchocephalians, ruling reptiles, lizards, and snakes derived by loss of one or both temporal arches. Abbreviations; j. ipsgl; p. parietal; po, postorbital; sq. squamosal.

traction, may develop high on the side of the cheek, in a low position, or in both—the last being termed the diapsid condition, because of the two bars of home left on the cheek after fenestration. Stem reptiles have no temporal openings, and the same is true of chelonians, although the roof may be "caten away"—i.e. emarginated—to give a result comparable to fenestration. Such extinct regises as the plesiosaurs and ichthyosaurs have an upper opening. A great majority of reptiles, alive and extinct, are diapsid types. This is true of the tuntara—Sphenodon—and of the whole host of archosaurian reptiles with the crocodilians as living representatives, the birds (Fig. 162, 4) are diapsid in pedigree, but the cheek bars, external to the swollen braincase, have largely disappeared. Lizards and snakes are descended, too, from diapsid ancestors, but in lizards the lower of the two bars has gone, and in snakes both have vanished.

In the ancestry of mammals (Figs. 163, 164) there developed a single temporal opening which at first was relatively small and low down on the cheek. In later forms the opening gradually enlarges to include nearly the whole cheek area, and even the bar behind the orbit is broken down in most mammals (it may be rebuilt later, notably in primates). In a typical mammal, the remnants of the original skull roof and cheek behind the orbits includes only (1) the narrow syg-

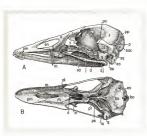


Fig. 162. d. lateral, and B. sentral views of the shall of a duck (Anna). Abbreviations: a, angular, bo. basioccipital; bo. basisphenoid: d. dentary: en, external naris; eo, exocepital; f. frontal; i.a, internal naris; j. jugal; l. lacrimal; b. laterosphenoid, en maxillar, nasasi, p. parietal; f., palatine; pm. permentilis; po, postorbital; pp. postaparietà; p., parasphenoid; p. pereygoid; eo, supraoccipital; sq., squamosal; s. vomer, (After Hellman).

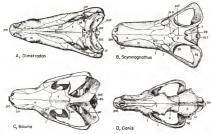
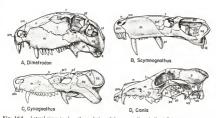


Fig. 16.3. Dorsal views of skulls to show the evolution of the mammalian skull roof. A Primitive curity Permin mammal ancestor (pelycosaury), B, a later Permin therapolit, C, a progressive Traissic therapolit, D, the dog. Abbreviations: e, excecipital, F, frontint, j. jougl. L, incrimal; e, manulia, e, assair, ecc. eccipital bone; p, pariental parametr, p. postfornth; pm, perminalit; pm, postportical; pm, postportical;



matic arch below the area covered by temporal muscles and, in such a form as the dog, (2) the restricted region in the midline of the skull roof which may form a sagittal crest. At first sight one tends to think that the area covering the side walls of the expanded braincase (formed mainly by extensions of parietal and frontal) is a part of the external skull surface and that the xygomatic arches are excreseences added to the outside (like handles on a jug); however (as discussed later) these lateral surfaces of the braincase are not part of the original expanse of the roofing bones but newly developed deep flanges; they lie deep to the jaw muscles, whereas the original surface was superficial to them.

While the temporal openings were developing in the phylogeny of mammals, there was a concomitant reduction in skull roof elements. Intertemporal and supratemporal disappear early, followed by loss of the septomaxilla and quadratojugal; postparietal and tabulars are incorporated in the occipital bones; the five original elements surrounding the orbit are reduced to jugal and a small lacrimal, and the maxilla is greatly enlarged in connection with development of the large canine teeth. Through the span of the series of extinct mammal-like forms we see—with fenestra development, loss of elements and changes in proportions—the gradual development of the familiar pattern of the mammalian skull.

The Palatal Complex in Tetrapods. In modern amphibians (Fig. 165, B-D) the original dermal elements of the palatal complex are retained, except for the posterior lateral element—the ectopterygoid—but the quadrate may be incompletely ossified and the epipterygoid is absent; further, the originally movinompletely ossified and the epipterygoid is absent; further, the originally movinompletely ossified and the epipterygoid is absent; further, the originally movinompletely ossified and the epipterygoid is absent; further, the originally movinompletely ossified and the epipterygoid is absent; further, the originally movinompletely ossified and the epipterygoid is absent; further, the original of the experiment of the experiment

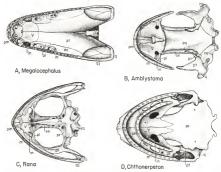


Fig. 165. The palate of amphibians. A, Paleozoic labyrinthodont; B, a salamander; C, a frog; D, an apodous amphibian. Abbreviations: ee, ectopterygoid; eo, exoccipital; in, internal maris; m, maxilla; pl., palatine; pm, permaxilla; pr, procoic; pp, parasphenoid; ps, pterygoid; q, quadrate; qj, quadrate; qj, quadrato; quad

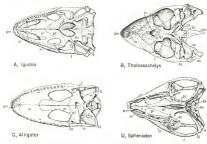


Fig. 166. The palate of reptiles. A, Lizard; B, a sea turtle; C, a young alligator; D, Sphenodon, Abbreviations; bo, basioceipials; ba, basisphenoid; ee, ectopterygoid; in, internal naris; j, jugal; m, maxilla; op, opisthotic; pl, palatine; pm, premaxilla; ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadrato-jugal; soe, superaoceipital; qs, squamosal; e, vomer.

able joint between braincase and palate is lost and the two are immovably fused. In frogs the anterior end of the braincase is narrow, and there are very large interpterygoid vacuities. In the other two orders the floor of the braincase, covered by the parasphenoid, is very broad and flat and the vacuities on either side less developed in consequence. In reptiles (Fig. 166), early types held fairly close to the primitive conditions. The Squamata and Sphenodon have modestly developed interpterygoid vacuities and retain the original motility of palate on braincase, but in other groups the two structures fuse together in the sphenoid region, and the palate tends to become a solid plate for its entire width. The reduction of temporal arches in the Squamata has enabled the quadrate to move freely on the remainder of the skull, and in snakes this, combined with flexibility of other jaw structures, gives them an enormous gape for swallowing large prev whole (Fig. 160, D, E). In some chelonians the internal nostril openings, placed far forward in primitive forms, lie in a pocket in the roof of the mouth with some development of a secondary shelf of bone below them. We see here the beginning of a secondary palate. This is developed to a much higher degree in crocodiles and alligators, in which the secondary shelf of bone is so extensive that the air channels extend far toward the back of the skull before opening into the mouth-a feature useful to these aquatic animals when dealing with prey under water. In birds (Fig. 162, B) the palatal structures are lightly built and flexible, with a movable articulation with the braincase and with freely movable quadrates.

In the line leading to mammals (Figs. 167, 168) the palate in the earliest forms was essentially that common to all early reptiles. However, marked changes occur in later stages. The two palatal plates become tightly welded to the sides of the braincase, with a loss of motility (and the little ectopterygoid vanishes). Anteriorly, there is a progressive development of a secondary palate, the two

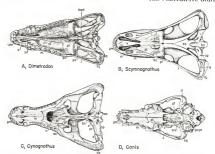


Fig. 167. A serice of skulls in ventral view to show the evolution of the mammalian pulate. A. Primitive early Permian pelyocoaury, B., a late Permian therapsid; C., an advanced Triasses therapsid; D. and the control of the principal changes include development of secondary palate in C. and D. loss of morable hash radulation and fusion of braincase and pulate in B.D. reduction of perception; loss of quadrate from skull structure and development of me sign spoint in D. address pulsa in D. Abbrevations: ab. auditory bulls; lost, head articulation of palate and braincase; bo, basiscicipital; do, basisphenoid; c. caple perceptide, et., excellent process propositions of palate and braincase; bo, palater; jugal, and marres; jugals, marres; jugals

maxillae and the palatines bridging the floor of the original vault of the mouth roof. Although never as extended as in crocodilians, this development, facilitating breathing concurrently with eating activities, was presumably highly useful to mammal ancestors in which uninterrupted breathing was becoming a functional necessity. Posteriorly, there is, in the line leading to mammals, a reduction of palatal elements. The epipterygoid disappears from the palatal structure (we shall presently find it associated with the braincase); the pterygoid has shortened to become (as its name implies) a wing-like process attached to the base of the braincase; the quadrate, small in therapsids, has in mammals abandoned its position in the skull to become an auditory ossicle (cf. p. 362). This last change is associated with the development, unique in manimals, of a new jaw articulation. As is noted in the final section of this chapter, the dentary bone of the lower jaw in advanced therapsids grew upward and backward to approach the squamosal at a point close to the original lower jaw articulation with the quadrate. In mammals a new socket for the jaw develops on the lower surface of the squamosal, and the quadrate bone has lost its original function.

The Braincase in Lower Tetrapods. In modern amphibians the braincase has tended to become broad and flat—more so in urodeles and apodans than in the frogs. With the skeletal degeneration seen generally in the three living orders, it has reverted in great measure to a cartilaginous condition. There are paired exoccipitals, often a proteic bone and, anteriorly, a sphenethmoid:

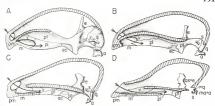


Fig. 168. Diagram to show the evolution of palatal structures and auditory ossicles from primitive requires to mammals. Longinizalian sections of skulls, with boxes of skull not and palate represented as if cut vertically just to the right of the midline thatched surfaces). The left half of the skull and the enter braincase removed, so that the plantal structures of the right side are seen in medial view. In addition, the stapes and the articular element of the lower jaw are ignored to show the evolution of the audition of the stapes and the articular element of the lower jaw are ignored to show the evolution of the audition of the stapes and the articular element of the lower jaw are ignored to show the evolution of the audition of the stapes of the primary of the stapes of the control of the control of the multi-like policy of the stapes of the control of the control of the control of the dependence of the control on the epipherygoid is in B. the polate becomes fixed to the brain ease; the epiperygoid is reduced to the ignaniant and articular, forming the articulation between upper and lower jaws are reduced in size and lose their original function but survive as auditory ossieles. Abbreviatione a, articular, as, alsphenoid; e, epiperygoid; ee, exupterygoid, e, incurs en, maxille; me, mulleus; pl. platine; pm, premaxille, pt, pterygoid, e, quadrates, subpres; e, vomes.

other ossifications have disappeared. The occipital condyle, originally single, is paired in living amphibians, and the skull has apparently shortened posteriorly, for in the occipital region the twelfth cranial nerve (the hypoglossal) is no longer present. Reptiles, on the other hand, show in many instances a much better relation of primitive features: there is usually no flattening of the braincase, and ossification is much better than in modern amphibians; with one exception, every primitive bony element of the braincase is still present. The condyle remains single in all typical reptiles, and reptiles retain a hypoglossal foramen. There is one major difference from a primitive amphibian presumably because of the relative narrowness of the skull, the two orbits are close together and the narrow braincase region between them fails to ossify; the old sphenethmoid ossification is reduced or absent (although partially replaced in snakes and crocodites by a new element, the laterosphenoid.). In brinds (Fig. 162, p. 186) the swollen braincase is completely surrounded by bone, because of a process of new development of hony plates comparable to that desertible debox for mammals.

The Mammalian Braincase. In mammal-like reptiles the braincase clements were those seen in early amphibians and primitive reptiles. When the mammalian condition is attained, notable changes have occurred (Figs. 169, 172). The condyle (as in modern amphibians) is now double rather than single, and the occipital bones have fused in the adult into a single occipital element (to which dermal ossifications from the back of the skull have been added). The ear capsule, primitively formed by two bones, now consists in the adult of a compact

fused structure, the periotic. This is situated low down at the side of the brain-case wall; it may project posteriorly to form a mustual process, adjacent to which there may be a projecting paroccipital process of the occipital bone. The middle ear cavity, containing the delicate ear ossicles, lies just external to the periotic, with the ear dumm at its outer surface. With the result of protecting these delicate structures, there is developed in placental mammals an ossified auditors bulla. This always includes a dermal element, the varpanie bone, which forms a ring around the eardrum and may complete bulla formation; in many mammals, however, a second small element, the entoty mpanic, performed in cartilage, makes up the deeper part of the bulla. The embryonic story indicates that the tympanie bone is a former element of the reptile lower jaw which had lost its original function and has been "pilfered" by the skull; the entotympanic, however, is a new structure. In many mammals periotic and bulla fuse, in the adult, with one another and with the adjacent squamosal to form a compound element termed the temporal bone.

The basisphenoid persists in the pituitary region of the braincase floor, it often fuses with neighbors (alisphenoid, presphenoid, orbitosphenoid) to form a compound element of small size but complex structure termed the sphenoid. Farther forward the braincase floor is continued by a small surviving part of the sphenethmoid, the presphenoid, of which lateral wings are termed the orbitosphenoid. The presphenoid may continue to the front end of the brain cavity, but in a number of mammalian orders this region is formed by a new braincase element, the mesethmoid bone. The olfactory nerve fibers enter the brain cavity from the nasal region through the sievelike cribriform place, developed in whichever of the two bones last mentioned forms the naterior end of the braincase. In the nasal region, we may note, scrolls of cartilage or bone, turbinals, are developed from the nasal causale and attached to the elements bounding the nasal chamber.

The bones so far named include the entire roster of elements formed in the braincase proper. But if we examine the actual "braincase" of a typical mammal (Fig. 169) it will be seen that they form little but the floor and the back wall of the brain cavity (Fig. 170). The mammalian brain has expanded to such proportions that the braincase proper has been unable to keep up with its growth; most

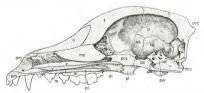


Fig. 169. Median sagital section of the dog skull. Diagonal lines indicate sectioned bones. It will be seen that most of the bone enclosing the brain cavity is derived from dermal elements (f. p., sq), and even part of the occipital is embryologically of dermal origin (cf. Fig. 171). Abbreviations as, aliaphenoid; f. frontal: m, maxilla: me, mesethmoid: n, misuk occ, occipital: p. parietal: per, perfolic; p.h. palitice: pm, prematilla: per, perfolic; ph. palitice: pm, prematilla: per, perfolic; ph. palitice: pm, prematilla: per, perfolic; ph. palitice: pm, prematilla: per, perfolicit.



Fig. 170. Diagrammatic dissection of the dog skull in lateral view. All dermal bones of the skull ord are removed (including the demand component of the occipital), leaving a series of hones comparable to those of the palatal series and braincase of Figure 151, D. Bermal publated elements include voner, palatice and percyclic the allegabenoid (= priparyogio) is a cartilage bone palatal element. Elements of braincase origin include mesethmoid, prophenoid (plas orbitosphenoid), paintenand, percis can almost of the occipital bone. The upper margin of the brain carely is shown in outline, and the formal control of the comparable of the control of the percis of the percision of

of the walls of bone surrounding the brain in the adult mammal have been derived from other sources.

In primitive mammal-like reptiles (Fig. 171, A) the parietals and frontals, lying above the brain, had been much reduced in extent, owing to the enlargement of the temporal fenestrae. In therapsids and mammals they have, however, redeveloped by sending deep flanges downward beneath the temporal muscles to cover much of the upper and lateral surfaces of the expanded brain (Fig. 171, B, C); as is obvious from the figures, these new surfaces are not part of the original skull roof, but are new developments in a deeper plane. But even with this development, a gap would still be present in the lateral skull walls had not advantage been taken of still another possibility. The old reptilian epipterygoid, part

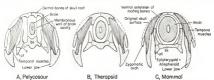


Fig. 171. Diagrammatic cross sections of the skull and jisss of A, a primitive manufable registe. Be an abstraced nummable file form, and C, a manufable to bose features in the development of the skull roof and braincase. (1) Part of the lateral walls enclosing the expansing brain were originally menhanous. This lateral area comes to be embeathed by verated excessions of the roofing homes and by the incorporation of the epiptergoid of the palant structure as the aliaphronid. (2) This extension of the roof in bone downward around the brain gives the appearance in manufacts of their the original stuffure, however, by external to the temporal muscles, as indicated by the broken the properties of the properti

of the palatoquadrate cartilage, originally formed the articulation between palate and braincase. When, in the mammal-like line, palate and braincase were fused, its original function was lost. It persisted, however, as a small platelike structure: in mammals it has been "plastered" into the braincase to fill the remaining gap in its lateral wall as the disphenoid bone.

In sum, the expanded brain capsule of a mammal is a composite affair. The original braincase is able to do little more than form its floor; dermal elements of the roof and the alisphenoid, "borrowed" from the palate, are called into play to form the walls and roof of this expanded structure.

Mammalian Braincase Foramina (Fig. 172). We have mentioned earlier the various openings for nerves and vessels found in the braincase of lower tetrapods. The situation may be reviewed for mammals, for although many of the openings are the same, the nomenclature (unfortunately) differs; further, the incorporation of the alisphenoid and auditory bulla has modified the nature of the braincase walls.

Certain of the foramina and canals seen on the surface of the skull do not enter the braincase. In this category we may note: the incisite foramina in the front of the palate in some mammals, which connect the mouth with the vomeronasal organ (cf. p. 346); the infraorbital foramen (sometimes enlarged to a canal) which carries nerves and vessels forward from orbit to snout; the nasolacimal canal, containing the tear duct; the disphenoid canal piercing the bone of that name in some forms and carrying a branch of the internal carotid artery forward onto the palate; the external auditory meatus leading out from the cardrum; the opening into the bulla for the custachian tube; the canotid canal through which the internal carotid runs forward beneath the bulla.

Of openings between surface and brainesse may be listed: the optic foramen in the orbitosphenoid for nerve II; the anterior lacerate foramen, in front of the alisphenoid, typically transmitting nerves III, IV, VI and part of V; the foramen rotundum and foramen orale usually piercing the alisphenoid bone and carrying other branches of nerve V; a middle lacerate foramen back of the alisphenoid through which the internal carotid artery enters the brain cavity; the stylomatosid foramen back of the ear bulle, by which nerve VII reaches the surface after a

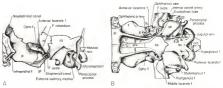


Fig. 172. Braincase region of a dog in A. lateral view, B. ventral view, to show foramina. In B are indicated the main nerves, the course of the internal carotid artery and its palatine branch and the jugan view in. Abbreviations: da, adulary politic, a, slapshenoid; δρ., bassice/pitals, δ. hassispe/pitals, f. foothit. j. jugal; m. maxilla; oer, occipital bone; pl., palatine; prs, presphenoid; pt., ptergoid; sq. squamosal; r. vomer.

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tortuous passage through the periotic and bulla; the jugular or posterior lacerate foramen between otic capsule and occipital bone, through which emerge nerves IX–VI and the internal jugular vein; and the hypoglossal foramen (sometimes multiple) in the occipant for nerve XII. In addition, openings from the brain cavity which do not reach the surface include the multiple openings piercing the cribriform plate for nerve II, and the internal auditory meatas, through which nerve VIII leaves the braincase and enters the ear capsule and through which nerve VII begins its outward journey.

Lower Jaw (Figs. 173, 174). To conclude this chapter we may turn (with relief) to the relatively simple story of the evolution of the lower jaw. As we have noted, this may have begun its history as a part of a gill arch which in the sharklike fishes forms the mandfulular cartilage. In all vertebrates with bony skeletons, however, this is reinforced and largely replaced functionally by a series of dermal elements. The cartilage develops fully in the embryo, but usually produces in the adult only a single bony element, the articular, situated at the back of the jaw and bearing, as the name implies, an articular surface for the quadrate bone of the skull.

Of sheathing bones on the outer surface, the most important and largest is the *dentary* bone, which bears the marginal tooth row and forms part or all of

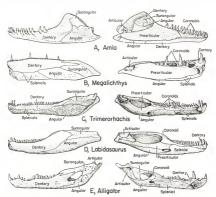


Fig. 173. Left lower jaws, outer views at left, inner views at right, of A, a ray-finned fish, the bow fine B, a primitive crossoperygane, C, a primitive labyrinthodout; D, a primitive reptile; E, an alligator. The jaws of modern teleosts, amphibians, and reptiles, in which the number of elements is reduced, have been derived from the types shown in A, C, and D, respectively.

the symphysis uniting the two jaws. Below and behind the dentary in many primitive fishes and early tetrapods is a whole series of dermal bones on the outer jaw surface: two splenial elements, an angular and a surangular. On the upper surface of the jaw, in front of the short articular bone there is a fossa into which the major muscles closing the jaw insert and into which enter blood vessels and nerves serving the jaw. Below this fossa, on the inner side, there primitively runs forward a long prearticular bone; below the dentary there is primitively, on the inside of the jaw, a series of three slender coronaid bones, often hearing teeth. The lower part of the inner surface of the jaw is often sheathed by extensions of the bones of the outer surface.

From this primitive structure there are numerous variations, too great in number to be recounted in any short space; almost all involve reduction in the number of elements present. The dentary is almost invariably retained, and the articular, because of its function, is present in all groups except mammals (although it fails to ossify in some skeletally degenerate fishes and amphibians). On the other hand, there is seldom more than one splenial; the coronoids are usually reduced in number and may be lost; angular, surragular and peratricular are more constant, but even these may be absent or fused with neighboring elements. A few variants in jaw structure among fishes and lower tetrapods are shown in Figure 173.

In the evolution of mammals (Fig. 174), we find in the fossil therapsids a steady increase in the size of the dentary and a corresponding decrease in the size and strength of other elements. In advanced therapsids the enlarged dentary

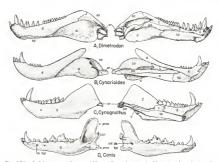


Fig. 174. Left lower pass of mammal-kile reptiles and mammals, illustrating the reduction of μs elements. Outer views (efg) and inner views (efg)b). A Primitive mammal-kile reptile (pelycosun); B. a primitive therapsid; C, an advanced therapsid; D, a typical mammal (dog). Abreviations: a, angular a proc, angular process; ar, articular; ε, cornoach; con, condyler, e, proc, cornoad process; d, dentar; and be for, inferior dental formers; no fee, meatal foremers, pa, peraircular, sa, surangular; pa, splenial.

has developed an ascending coronoid process to which much of the jaw musculature attached, and posteriorly reaches back to a point close to that at which the articular element gains contact with the skull. The remaining jaw elements are small and feeble structures plastered on to the inner surface of the dentary. With the transition to the mammal condition, these elements disappear from the jaw, which now consists of the dentary bone alone. The old elements are not, however, entirely abandoned. As will be seen later the articular takes up a new if modest career as a tiny ear ossiele (cf. p. 362), and it appears probable that the angular bone has been incorporated into the skull as the tympanic bone of the auditory bulla.

# 9

## MUSCULAR SYSTEM

The muscular system, judged quantitatively, at least, should loom large in any study of the present sort, for muscle tissue constitutes from a third to half of the bulk of the average vertebrate. Functionally, too, the musculature is of the highest importance. From locomotion to the circulation of the blood, the major functions of the body are caused by or associated with muscular activity. Movement—of trunk, limbs, jaws, of an organ or an organ part—is the major product of this activity, but muscular work may be expended in negative fashion in maintaining body stability and is of primary importance in the production of body heat. And the activity of the nervous system—even the highest functioning of a human brain—has little mode of expression other than the contraction of muscle fibers.

Muscle Fiber Types (Fig. 175). Histologically, two major categories of muscular tissue may be distinguished—smooth and striated fibers. Smooth muscle fibers are the simpler and smaller of the two types. They are normally derived from embryonic mesenchyme, in association with the connective tissues. The main site of smooth muscle fibers is in the lining of the digestive tract, or of its embryonic outgrowths such as the traches and bronchi of the lungs, and the bladder. Still other loci, however, are independent of the gut—notably the walls of circulatory vessels. A typical smooth muscle fiber is a slender, spindle-shaped body, averaging a few tenths of a millimeter in length. There is a single centrally situated nucleus; with special stains the seemingly homogeneous protoplasm exhibits tiny fibrils running the length of the cell. As the name implies, the fibers in this type of muscle lack the cross-banding seen in striated muscle cells. Smooth muscle fibers may be scattered, but more generally are arranged in bands or bandles, with interspersed connective tissue fibers uniting them into an effective common mass (cf., for example, Figs. 250, 253, pp. 262, 269).

In the heart is found a special type of cardiac muscle not present elsewhere. Embryologically heart muscle is of common origin with smooth muscle, but in correlation with its important functions and constant activity, it has developed a cross-banding similar to that seen in strated fibers. In contrast with that tissue, MUSCULAR SYSTEM 199

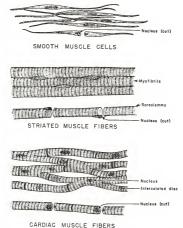


Fig. 175. Major types of muscle fibers. (From Hunter and Hunter, College Zoology.)

however, heart muscle does not consist of individual fibers, but is a continuous network of dividing and recombining strands, in which at intervals are situated prominent cross bands, termed intercalated discs, which separate successive cellular units.

Strated muscle fibers form the "flesh" of the body, the voluntary muscles, derived in great measure from the myotomes of the embryo; they generally at tach to and move skeletal structures. These fibers are large, multinucleate cells, with lengths which vary from about a millimeter to a number of continuers. As in smooth muscle, the fiber contains a large number of closely-packed longitudinal birshs. The striated appearance is due to the fact that the fibrils consist of alternating light and dark portions which occur at the same point on each fibril; changes in the banding occur between relaxed and contracted phases of a fiber. The banding is shown in more detail in Figure 176. It is currently believed that the banding is due to the alternation in the fiber of two types of fibrils, composed of the proteins myosin and actin; neither type extends the full length of a "segment" of the banding, and contraction consists of the sliding of one series on the other so that the total length of each "segment" is reduced. Striated fibers are

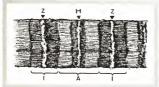


Fig. 176. The banding of a striated muscle fiber. Alternate light and dark bands (A, I) are present within each, further markings may be distinguished, particularly a crossband, H. within A, and Z within I. (The fiber as drawn here was viewed under polarized light; with ordinary illumination, the A band is dark, the I band light!) (From Guyton, after Sewell-Voyègyi.)

arranged in parallel fashion to form muscles. Connective tissues run between the fibers and bind them together, form sheaths for fiber bundles and, further, form an external sheath for the muscle as a whole.

The force of a muscle is everted through a contraction of its fihers, and this is in tura caused by folding of the contained fibrils. In smooth muscle the contraction is relatively slight and slow, but may be long sustained; striated muscle may be stimulated rapidly and contract vigorously, but is more readily fatigued. A great and speedy release of energy is required for muscle contraction. In the long run this energy is supplied by consumption of carbohydrates present as glycogen in the fibers. However, it appears impossible to oxidize glycogen with sufficient rapidity, and special chemical mechanisms are developed. Muscle fibers are notable for the presence of considerable amounts of adenosine triphosphate (ATP), remarkable for its ability, through loss of part of its phosphate, to release energy rapidly and in quantity. However, for continued "work," the phosphate must be rebuilt and energy supplied for the process; this is done by a "normal" oxidization of glycogen. If activity of the fiber is too great and too continuous, the glycogen cannot be utilized efficiently and the muscle is "fatigued."

A muscle as a whole may contract slightly or strongly, briefly or for a considerable period of time; the result varies according to the number of fibers stimulated by the nerves and the rapidity of the stimuli. Individual fibers, however, work on an "all or none" basis; each fiber either contracts as fully as possible or fails to contract at all. The sharp contraction of a striated fiber and the more gradual relaxation which follows take altogether but a tenth of a second or so. Normally, however, muscle contraction is due not to a single stimulation but to a continuous tattoo of nerve impulses. A second impulse given before the effect of the first has worn off will increase the contraction, a third will further increase it, and a long series may bring the muscle fibers to a state of maximum contraction or tension (tetanus).

Classification of Muscle Tissues. How may the varied muscle tissues of the body be classified? One obvious suggestion is to do this on the basis of histologic structure, with striated and smooth (including cardiae) muscles forming the two main divisions. This at first sight seems reasonable, for in addition to the differences between fiber types, we find that striated muscles are generally under voluntary control, whereas smooth muscles are under the influence of involuntary enercy, striated muscles are mostly formed in the "outer tube" of the body, smooth muscles are associated with the gut; most striated musculature is derived from somities, while smooth muscles comes from mesenchyme.

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One prominent group of muscles, however, is in many ways anomalous and ruins the seeming simplicity of such a classification. This is the branchial system of muscles, primitively associated with the gill bars and prominent in the head and "neck" region of all vertebrates. These muscles are striated and under voluntary control. But they do not come from myotomes; they arise, rather, from mesenchyme of the splanchnopleure, like smooth muscles; they are associated with the gut, as are typical smooth muscles, and their innervation (as will be seen in Chapter 16) is by nerves more closely comparable to those supplying the smooth muscles than to those running to typical striated musculature.

All this suggests a picture of the primitive vertebrate as having had two discrete sets of masculature. The first, which we may term the somatic musculature, forms the muscles of the "outer tube" of the body, is universally striated, is typically developed from myotomes, is innervated by a somatic type of motor neuron (5, 375) and is associated functionally with the adjustment of the organism to its external environment. To this group belong the typical muscles of trunk, tail and limbs (and, incidentally, those of the eyeball). The second group is the risceral musculature, connected mainly with the gut tube, derived not from myotomes but from mesenchyme, innervated by visceral motor nerves and mainly associated with digestion and other functions of the animal's internal economy. In this second group the musculature in the posterior part of the gut has retained a simple structure of smooth muscle fibers; in the head and pharyngeal region, however, eating and breathing functions have necessitated the development of the more vigorously-acting straied type of muscle.

It appears, then, that despite the seeming impropriety of associating in one major group all smooth and some striated elements, the most natural classification of muscles is as follows:

	Trunk and tail
Somatic	Axial
Visceral	Branchial (striated) Smooth (gut, and the like)

The smooth muscles are, in general, component parts of various organs and need no separate consideration here. We shall in this chapter discuss only the formed muscles of striated type—the various somatic muscle groups and the branchial muscles of the visceral system.

Muscle Terminology. As with other organ systems, muscles are given, as far as possible, names used in human anatomy. However, we are in doubt in many cases as to the homologues of human muscles in lower vertebrates. Another, and safer, procedure when in doubt is to give muscles of lower vertebrates names which are simply descriptive of their general position or attachments. Thus, for example, a muscle in reptiles running from ilium to femur may be homologues with part or all of the glutteal muscles which lie in somewhat the same position in a mammal; but since doubt exists, trouble may be avoided if we simply call the reptile muscle the iliufosmoralis.

There are various terms frequently used to describe muscles, particularly

limb muscles, according to the type of action they perform. An extensor acts to open out a joint, a flexor closes it. An addactor draws a segment inward, an abductor the reverse; a levator raises a structure, in contrast to a depressor. A pronator or supinator rotates the distal part of a limb toward a prone or supine position of the foot (i.e., with palm or sole down, or the reverse). Constrictor or sphinteer muscles surround orifices (as gills, cloaca) and tend to close them when contracted.

Muscles usually attach to skeletal elements at either end. The more stable attachment is the area of origin, the other the insertion; in limb muscles the proximal end is always considered the point of origin. A muscle with multiple heads may be termed bicipital, tricipital and so forth. Often muscles originate directly from a broad surface of bone or cartilage, and we then speak of a "fleshy" origin; in many cases the muscle terminates at one or both ends in a tendon or a flat sheet of connective tissue— an aponeurous or fuscia.

Muscle Homologies. The comparative study of musculature is difficult because of the variability of muscles and the apparent ease with which their relations and functions may alter. A muscle which is a unit in one animal may be split into two or more distinct muscles in another, and there are cases in which originally distinct muscles have secondarily fused. Embryologic origin is here, as ever, an important criterion for the determination of homologies. In many cases, at least, groups of individual muscles in the adult can be traced back to larger aggregations of muscular or premuscular tissue in the embryo (cf. Fig. 1838, B. p. 209), and the mode of breaking up of these mother masses gives valuable evidence of homologies.

The motor innervation of muscles provides valuable clues. It was long believed by many workers that there was an unalterable phylogenetic relationship between a given nerve and a given muscle. Embryology, however, gives no indication that there is any mysterious affinity between specific nerve fibers and the specific muscle fibers which form a given muscle, and in some few cases it sense quite certain that the innervation of a muscle is distinctly different in different animals. Nevertheless, actual practice indicates that the nerve supply to a particular mass of muscle does tend to remain constant, and that innervation affords an important clue to muscle identity.

### AXIAL MUSCLES

Trunk Musculature in Fishes. The major part of the somatic muscle division, in fishes, is the axial musculature, arranged for the most part in segmental masses along the flanks (Figs. 177, 178, A. B). It forms the major locomotor organ of a fish; by rhythmic, alternate contractions of the muscles of the two sides the fish's body is thrown into propulsive waves (cf. Fig. 120, p. 148).

The axial musculature is, in fishes, of direct myotomic origin, as can be seen, for example in the embryo of a shark (Fig. 179). The segmental arrangement is in great measure retained in the adult, most of the trunk musculature being arranged in myomees which correspond in number to the vertebrae and alternate with them. The muscle fibers in each segment are oriented anteroposteriorly; few fibers attach directly to skeletal parts, but insert into stout sheets of connective tissue, the myocommata (Fig. 114, p. 144), which lie between successive myomeres and reach inward to tie into the vertebral column; it is in the myocommores and reach inward to tie into the vertebral column; it is in the myocommores and reach inward to tie into the vertebral column; it is in the myocommores and reach inward to the into the vertebral column; it is in the myocommores and reach inward to the into the vertebral column; it is in the myocommores and reach inward to the into the vertebral column; it is in the myocommores and reach invariant to the contract the contract the contract the contract the contract the contract that the contract th

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Fig. 177. Dissection of a salmon to show axial musculature. In four places a series of myomeres has been removed to show the complicated internal folding of these segmental structures. Within the body each Y projects farther anteriorly or posteriorly than it does at the surface. The lateral septum is visible, cutting the main, anterior-pointing V. (After Greene.)

mata that the ribs (and the extra intermuscular bones of teleosts) are developed. In the embryo the myomeres begin as simple vertical banks, but in the adult they are folded in a zigzag fashion which appears to promote muscular efficiency. In Amphioxus each fold is a V, with the point turned forward along the flank. In most fishes there is greater complexity, to give the shape of a W with its upper edge turned forward; deep to the surface each myomere may run some distance force and aft, overlapping and underlapping its neighbors (Fig. 177).

In fishes above the cyclostome level there develops a horizontal septum of connective tissue running fore and aft just below the tip of the anterior-pointing Vs; it is at the points of intersection of this septum with successive myocommata that dorsal ribs develop (Figs. 2, B. D. 6, 114, p. 1, 244). The axial muscles of gnathostomes may be divided into two major groups: the peaxial musculature lying above the septum and above (or external to) the dorsal ribs, and, below the septum, the hypaxial musculature (Fig. 178). Apart from the main mass of fish axial musculature, lesser muscless may be developed in connection with the median fins. Further, regional specializations, most highly developed in land vertebrates, may be found in the tail and, particularly, in the region from the shoulder girdle forward. Below, we shall first follow the history of the main trunk muscle groups—peaxial and hypaxial—from fishes upward through the tetrapods, and then return to pick up the story of more specialized anterior and posterior regions.

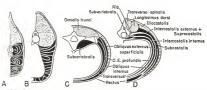


Fig. 178. Diagrammatic sections to show the divisions of the trunk musculture in  $A_a$  shark half. B, the shark trunk:  $C_a$  suredete:  $B_a$  a lizard. The epaxial muscles are stippled, hypaxial muscles in black. In D a rib is assumed to be present doesally, and the adjacent parts of the hypaxial muscles are labeled as in the rib-bearing region; more ventrally the names are those of the corresponding abdominal muscless. (Mainly after Vshib.)

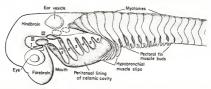


Fig. 179. A diagrammatic view of a shark embryo to show the development of the muscles. Skin and gut the removed the havin and eye and car varielise are included as landmarks. Postroirely, two tones have extended downward to form myomeres; in the region of the pectoral fin, paired hash are forming from neighboring myotomes apportain fin muscles. Ametrior to his, hads from anterior myotomes extend ventrally to form hypobranchial muscles. In the car region, myotomes (troken likes) are rudinentary or sheet, that first for horse of the most driven myotomes of the III) persist to form eye muscles to possible the position of the spiracular slife (s) and normal gill slife (2 to 6) is indicated. These interrupt the continuity of the celona and its peritoneal epithelium. Bads of this project upward abetween the gill slife with the project upward abetween the gill slife to the most position gill arches, the part after Braus-).

Epaxial Trunk Muscles. The dorsal musculature has led a relatively uneventful phylogenetic career. In fishes (Figs. 177, 178, A, B), it is generally a
massive column of segmented musculature which shows little signs of subdivision
and may be termed as a whole the dorsalis runci muscle. In land vertebrates it
s generally reduced in extent and restricted to a dorsal channel lying above the
transverse processes and the vertebrae. Simple in urodeles (Fig. 178, C), it tends
in ammiotes to be divided transversely into several longitudinal subdivisions such
as those seen in Figure 178, D. In turtles, with development of the shell, these
dorsal trunk muscles (and the ventral ones also) are much reduced, and they are
reduced in birds as well; in sankes, on the other hand, resumption of major locomotor functions by the axial muscles has resulted in a high development of these
dorsal muscles.

Hypaxial Trunk Muscles. In fishes, the hypaxial musculature of the trunk is essentially a unit, extending downward from the horizontal septum on either flank around the body wall (Fig. 178, B. In land vertebrates the thickness of this wall—and consequently of the hypaxial musculature—is much reduced; these muscles are, however, complex in structure (Figs. 178, C, D, 180, 181). We may distinguish three major subdivisions.

- Subvertebral muscles, dorsally and medially;
- 2. A lateral series of muscle sheets along the flanks;
- A rectus group ventrally.

The subvertebral musculature is generally small in volume and unimportant in function, acting merely in opposition to the dorsal musculature in dorsoventral movements of the spinal column.

The flank muscles, extending over the region from the transverse processes down to the ventral territory held by the rectus system, are complicated and varied. There are typically three superimposed major sheets of segmentally arranged muscle (each of which may be subdivided, however, in various regions and areas).

In urodeles, where ribs are absent, the three layers are: an external oblique muscle, whose fibers run essentially anteroposteriorly, but slant somewhat upward anteriorly; an internal oblique whose fibers, on the contrary, slant upward posteriorly; and, deepest of the three, the transverse muscle, whose fibers, in contrast to those of the obliques, run in a dorsoventral direction. In ammiotes a comparable series of simple muscle sheets may be present in the lumbar region, where ribs are short or absent. More anteriorly the transversus muscle usually persists, but the presence of the ribs breaks the two outer layers into a bewildering series of small muscles—intercostals, supracostals, subcostals and so forth (Fig. 181). To attempt to describe them in detail would be as tiring to the author as to the student.

The rectus abdominis primitively ran along the belly from shoulder region to pelvis as it does today in urodeles. At its lateral margins the rectus may be more or less continuous with the oblique muscles, particularly the internal oblique. In tetrapods with a highly developed set of sternal ribs the rectus is shortened and in mammals is estricted to the abdomen.

Mammals are notable for the development of the diaphragm, a partition separating thoracic and abdominal cavities and important in breathing (cf. p. 228). The diaphragm is moved by a series of thin muscle sheets which converge mis is boundaries toward its center, these appear to be specialized derivatives of the rectus musculature of the chest region.

Trunk Muscles of the Shoulder and Head Region. As might be expected, the forward extension of the trunk musculature is interrupted in great measure in the region of the shoulder girdle, and the specialized structures in

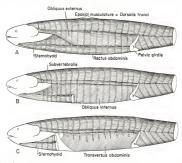


Fig. 180. Lateral views of the axial musculature of a urodele. A, Surface view (a thin superficial sheet of the external oblique, however, has been removed). B, The external oblique and rectus have been cut to show the internal oblique and subvertheal muscles. C, The internal oblique has been removed to show the transversus. (Modified after Maurer.)

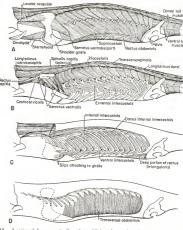


Fig. 181. A series of diagrammatic dissections of Sphenolon to show the anatomy of the axial mucless. In at this superficial sheet of the external oblighes has been removed. In B the supergrootshis, revise, throat muscless, and more superficial muscles to the scapula have been removed. In C the epacial muscles are can posteriorly, and the internal interesteals and triangularis on the six figured as indicated. In D the ribs are cut, and all other muscles removed to show the transversus. (Ather Mauurer and Firthinguez.)

the gill or neck region make for exceptional conditions in the anterior portions of the axial musculature. The dorsal epaxial muscles run forward with relatively little interruption past the shoulder to terminate at the occipital region of the skull; special slips may develop for head support. In addition slender elements of the subvertedral system run forward dorsally, but beneath the vertebrae.

The flank muscles—obliques and transverse—or their intercostal equivalents terminate anteriorly at the shoulder region. From the oblique series there develops, however, a very special group of muscles supporting the shoulder girdle in land vertebrates. Quite in contrast to the condition at the tetrapod pelvis, where the girdles are firmly fused to the backbone, the shoulder girdle has no direct connection with the column. The body is, instead, suspended between the two scapular blades in elastic slings formed by special flank muscle elements, the serratus and levator scapulae muscles. These run on either side from the top of

the scapular blade downward, in fan-shaped fashion, to attach to the anterior ribs or transverse processes (Fig. 181, A, B); through this pliable type of connection (analogous to the use of springs in automobile construction) the body is eased of much of the jolts and jars of locomotion. In mammals there is, in addition, a rhomboideus muscle, placed more dorsally, which tends to keep the upper end of the scapular blade in position by a pull toward the midline.

Although the flank muscles cease at the shoulder region, the ventral musculature, forming part of the rectus system, continues forward beneath the throat from the shoulder girdle. Such muscles in fish are known collectively as the hypobranchial musculature or coracoarcuales, for elements of this series typically originate from the coracoid region of the girdle and attach to the ventral end of the gill arch bars. In tetrapods various slips of this musculature persist as the sternohyoid, omohyoid and so forth (Figs. 180, 181, A). A remarkable development is associated with the fact that the tongue of land vertebrates develops in the floor of the mouth from the region of the gill arch bases. As it expands, it carries with it a mass of the hypobranchial muscle fibers present in this region; these consti-

tute the flesh of the tongue (Fig. 209, p. 232).

The embryology and nerve supply of the hypobranchial muscles are not without interest. As axial muscles, they are of myotomic derivation; however, the development of the gill slits separates the throat region from direct connection dorsally with the myotomes of the occipital and neck regions from which we would expect them to come. In some embryos, slips from these myotomes are seen in process of migrating circuitously backward above the gills, down behind the gill chamber, and then forward in the throat to form the hypobranchial (and tongue) muscles (Fig. 179, p. 204). We have noted earlier that there tends to be a constant nerve supply to a given mass of muscle, even if it has migrated far from its original position. In correlation with this fact we find that the hypobranchial muscles in fishes are innervated by nerves from the occipital region of the skull and the anterior part of the cervical region, which follow the same path of migration as did the muscle tissue, around the back of the gill chamber and forward along the throat. In amniotes comparable nerves form the hypoglossal nerve and cervical plexus; in the embryo these nerves follow the ancestral route back and down behind the embryonic gill pouches, and even in the adult they pursue a roundabout course to the throat and tongue (cf. pp. 386-387).

Caudal Muscles. In fishes, the axial musculature continues with little interruption past the cloacal or anal region into the tail. The epaxial musculature here is simply a continuation of that of the trunk. Ventrally, however, in the absence here of the body cavity and its contained viscera, the hypaxial muscles change from a series of sheetlike structures to a compact pair of ventral bundles

similar to the epaxial muscles above (Fig. 178, A, p. 203).

In tetrapods the great development of the pelvic girdles and the limb muscles arising from them has tended to break the continuity of the axial muscles between trunk and tail. The epaxial muscles may be little disturbed, but the interruption of the hypaxial elements at the girdle is complete, or nearly so. The tail, while not as important as in fish, is persistently stout and muscular in urodeles and many reptiles; ventrally, however, part of its volume is made up by muscles (the caudifemorales, described later) which run out anteriorly on to the femur and hence are limb muscles rather than true caudal muscles. Needless to say, the tail musculature is reduced in forms-such as anurans, birds, mammals and turtles-in which the tail as a whole is reduced in importance. From the



Fig. 182. Eye muscles. A lateral view, with the eyeball (in outline) removed; the ovals are the muscle attachments. The three eye muscle nerves are shown (III, IV, VI). (After Goodrich.)

ventral tail musculature just behind the girdle there usually develops in land vertebrates a sphincter muscle closing the cloaca or anal opening.

Eye Muscles. The muscles which move the eyeball form a far-flung anterior outpost of the axial musculature. Except in cyclostomes the series of mesodermal somites found the length of the trunk is interrupted anteriorly by the expanded braincase in the ear region; more anteriorly, small somites, usually three in number, persist in members of every vertebrate class in the region of the eye socket (Fig. 179). These play little part in the development of skeletal or connective tissues, but from them develop the muscles of the eyeball. Associated with these three somites, and innervating the muscles which they form, are three small cranial nerves—III, IV and VI of the numbered series (pp. 378, 385).

In most vertebrates six typical straplike muscles develop from these somites (Fig. 182). In the adult they take origin from the surface of the braincase and fan outward to attach to the eyeball; in varied combinations their pull will rotate the eye in any desired direction. Four of them, the rectus muscles, arise posteriorly close to the eye stalk or optic nerve, the other two, the oblique muscles, spring from the anterior part of the eye socket. Four of the six muscles are innervated by nerve III, the superior oblique by nerve IV, the posterior rectus by nerve VI. As this would lead us to suspect, we find that in the embryo four of these muscles usually arise from the first of the three eye somites, one each from the other two.

In addition to the six normal muscles, accessory ones may be present. In a majority of tetrapods (birds and primates are exceptions) there is a retractor bulb in muscle which tends to pull the eyehall deeper into its socket; in most amniotes there is a levator palpebrae superioris raising the upper lid, and rather variable slips which move the nicitiating membrane of the eye.

### LIMB MUSCLES

The musculature of the paired appendages is derived, historically, from the general mytonic musculature of the trunk and hence is part of the somatic system. The limb muscles, however, are so distinct in position and nature and so important in higher vertebrates that they deserve special treatment. In tetrapods, axial musculature declines in volume; the limbs and their musculature grow in most cases to relatively enormous bulk. To use a homely example, fish as food is axial musculature; in a steer, lamb or hog, the meat is almost entirely limb muscle, with little of axial origin remaining. Even a chop, in which the attached hone seems to testify to its axial nature, consists mainly of a limb muscle which takes origin from the trunk, and only the scrapings on the hone itself are really axial

As derivatives of the somatic system, limb muscles should, in theory at least, originate in the embryo from myotomes. In some lower vertebrates—specifically sharks—this origin appears to be demonstrable (Fig. 179), the paired fin muscles being derived from buds extending from the tips of a series of myotomes. In tetrapods, however, such an origin has not been demonstrated. The limb muscles arise from masses of condensed mesenchyme; it is, however, possible that this mesenchyme is of ultimate myotomic derivation.

In the fins of fishes the musculature is simple in construction (Fig. 183, B). Two opposed little masses of muscle are generally discernible, a dorsal mass serving to elevate or extend the fin, a ventral one to depress or adduct it. In addition there may be small slips developed from either group which give rotary or other special fin movement.

Tetrapod Limbs. In land vertebrates we meet with a different situation. The limb musculature is not only more bulky but more complex. The mode of development, however, affords a clue to a natural classification of the muscles present. Early in ontogeny, while the tetrapod limb is still a short bud from the body, a mass of premuscular tissue (Fig. 183, 4) is formed on both the upper and lower surfaces of the developing skeleton; it is clear that these two opposed masses are comparable to the dorsal and ventral muscle masses of the fish fin. From these masses arise all the complicated muscles of the mature limb; these muscles can, in consequence, be sorted out into two main series—dorsal and ventral, or (roughly) extensor and flexor series. In the distal part of the limb the distinctions between members of the two series are generally clear; in the proximal regions of shoulder and hip, however, various modifications would make a sorting out of these groups difficult were their embryonic origins not known.

To describe and compare in detail the highly varied musculature of all the tetrapod groups would require a volume in itself, which would be as exhausting as exhaustive. We will here confine ourselves to picturing and describing in brief fashion the major features of the musculature of a lizard, as representative of a fairly generalized primitive etrapod condition, and of an opossum as representing a basic mammalian type.

Pectoral Limb. Dorsal muscles (Figs. 184, 185, A, D). In all tetrapods

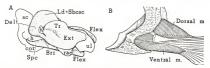


Fig. 183. A. External view of the left pectoral girdle and limb and its musculature in a litted embry (the skeleton unshaded, the musculature consists simply of supported part of not in a fish (start people). In the fish fin the musculature consists simply of uppened denset in the color masses. In the dalk limb vertebrate the limb has a large number of discrete muscles, in the color masses carranged in two opposed masses comparable to those of the fish fin. At the stage figured the two one are hardy beginning their differentiation into the muscles of the shull (c. Fig. 1884, 4.). The density is self-uppendix to the start of the shull be suffered to the start of the start o

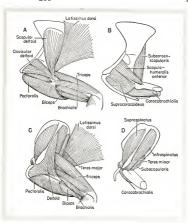


Fig. 184. Shoulder and upper arm muscles in the lizard (4, B) and opossum (G, D), lateral views; the right hand figures in each case are comparable deep dissections with latinsims, deltoid, pectoralis, and long muscles (triceps, biceps, brachalis); removed. Notable is the upward migration of the supracoracoideus to become the two "spinatus" muscles.

a number of dorsal muscles are present which attach to the humerus near its head and are responsible for much of the movement of that bone on the shoulder girdle. Two prominent superficial fan-shaped muscles of this sort seen in both reptile and mammal are the latissimus dorsi arising from the fascia of the flank and back, and the delabideus, taking origin (often in two parts) from scapula and clavicle. In mammals a slip of the former muscle has gained contact with the scapulo as the teres major. In reptiles a small external dorsal muscle, the scapulohumeralis anterior, is present deep to the deltoid; in mammals this has been pushed to the back margin of the scapula as the teres minor. In both reptiles and mammals a broad muscle (only partly showing in the figures) runs from the inner side of the shoulder girdle to insert on the humerus near the latissimus; this is the subcora-coscapularis of reptiles, the subscapularis of mammals.

These are the most proximal members of the dorsal or extensor series. Boydon, the dorsal surface of the humerus is covered by the triceps, which arises from the humerus and by one or more heads from the adjacent parts of the girdle; the muscle attaches distally to the olecranon of the ulna—this attachment is in fact the reason for the existence of that process—and serves to extend the forearm. Below the elbow the dorsal series is continued by the extensor series of the forearm. Most prominent is a complex sheet of muscles running downward from the elbow region and fanning out to the forearm bone and on to the hand;

a series of short extensors is present in the region of the "wrist" and digits. Lizard and mammal show much the same arrangement, except that in the latter a long extensor from the elbow has tendons, lacking in reptiles, running out directly into the digits.

Ventral Mescus (Figs. 184, 185, B, C, E, F). On the under side of the shoulder an important superficial muscle which gives a strong pull backward and downward on the humerus is the chest muscle, the pectoralist; this spreads fanwise far back over the sternum and ribs and inserts on a powerful process beneath the proximal end of the humerus. A deeper, smaller ventral muscle is the

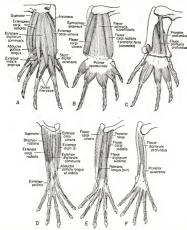


Fig. 183. Muscles of the foreram and hand in the limit (4 to C) and operatin ( $Do\ P$ ), conveited this grammatic and simplified. A and D are views of the extense surface, B and E superficial, Can B Affective dissections of the flevor aspect. On the extense surface the most prominent change from regille to manual is the reduction of short muscles on the manua and the development from the common extensor of trades to the toes. Long special muscles have developed for movement of the "thanh" and fifth digit in the libert aspect a prominent feature in repdies in the presence of a story and complete aponeurous from the libert aspect a prominent feature in repdies in the presence of a story and complete aponeurous clear to the test. In the contrast of the contrast of

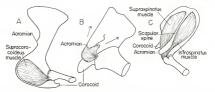


Fig. 186. Diagrams of the shoulder regions of A. a lizard, B. an embryonic opossum and C. an adultopossum, to show a major shift in shoulder measurabute between repiles and nameals and the conquent modification of shoulder gairdle structure. In the lizard the superconsoidess is a large ventral marcele running from conoxid plate to harmours. In the embryo opossum a comparable muscle is found, but this is, at the stage figured, treding to split and grow upward (arrows) on either side of the accomion. In the the adult manumal this muscle mass has become the derorally situated superspiratus and infraspiratus muscles; a new portion of the scapula has developed for the reception of the supraspiratus muscle, while the coracied has been reduced to a relability. (B sliter Charge.)

coracobrachialis, running from the coracoid bone to the lower side of the humerus. Ventral muscles with a flexor action opposing the triceps are the biceps and brachialis, extending along the humerus to insert on the forearm bones near their heads.

These four proximal muscles are present in fairly comparable form in both reptiles and mammals. But a fifth reptile muscle in this region appears, at first sight, to have no homologue in a mammal. This is the supraoracoideus, a large fleshy muscle which runs from the coracoid plate to the under side of the humerus. In the primitive sprawled tetrapod posture this muscle is important in keeping the body from sagging downward between the limbs. In mammals there is no muscle present in this position; indeed there is no coracoid plate from which it could arise.

The muscle, however, is actually present and prominent in the form of the supraspiratus and infraspinatus muscles on the scapula (Fig. 186); this major muscular migration is presumably responsible for the reduction of the coracoid region of the girdle, which originally afforded the muscle origin, and for the development of the spine and supraspinous fossa of the mammalian scapula. The reptile muscle has pushed its way upward beneath the delioid (as can be seen repeated in the mammalian embryo) and has (a) taken over the old scapular blade as the infraspinatus (and restricted the deltoid origin to the spine), and (b) occupied a new shelf (supraspinous fossa) built for reception of the derive supraspinatus muscle in front of the old anterior margin of the scapula. With the changed limb posture of mammals the supracroacoid ceased to function in its old position. It has, however, retained its supporting function by the insertion of the two hondogous mammalian muscles at the very tip of the humerus in front of the glenoid; the resulting lever motion tends to swing the limb downward and forward or, conversely, to pull the body up and back on the arm.

In the distal part of the limb, the main propulsive effort is a backward push of the forearm and digits accomplished by the muscles of the ventral, flexor surface, which are hence powerful in build. A series of long flexors fans out to the

forearm and wrist region somewhat in the fashion of the opposed extensors. But flexion of the digits is rendered difficult by the fact that muscles serving this function would have to pass round the curve on the under side of the wrist if they were to extend directly to the digits. This is avoided by the development of an aponeurosis, a pad of connective tissue beneath the wrist; to this attach the long flexors proximally and certain of the short toe muscles and tendons distally (a similar structure in the hind leg is shown in Figure 189). In mammals this pad of tissue is subdivided into several superimposed tendon sheets.

PELVIC LIMB. DORSAL MUSCLES (Figs. 187, 188, A. D). Certain of the dorsal muscles or nuscle groups in the hip and thigh region are readily comparable in lower tetrapods and mammals. Reptiles have a powerful fleshy pubo-ischiofomoralis internus (what names these muscles have!) which arises from the lumbar region and the inner surface of the girdle and inserts on the femur near its head; in mammals this develops as the iliacus and psoas muscles. Frequently grouped as the quadriceps femoris in both reptiles and mammals is a group of muscles which run down the femur to insert by a common stout tendon on the head of the tibia and extend the leg in much the fashion of the triceps in the "arm." The vasti muscles arising from the femur; heads aris

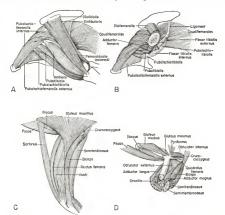


Fig. 187. Limb muscles of the pelvis and thigh in a lizard (A, B), and opossum (C, D), lateral views. A, C, Superficial views; B, D, dissections to show deeper layers of musculature.

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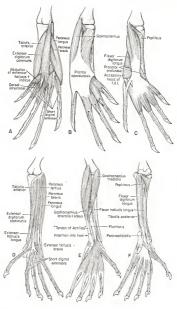


Fig. 188. Muscles of the lower leg and foot in a lizard (4 to C) and opossum (0 to F), somewhit diagrammatic and simplified. A and D are views of the extense surface B and E superficial, C and F deeper dissections of the floor aspect. The extenses surface of the lizard kind leg is comparable to that of the forearm and names except for a lesser development of individual massles on the inner (tibial = radial) side. In the change to mammals the modifications are similar to those seen in the front leg, in the contrast of the reduction from the common extenses and the development of low renders from the common extenses and the development of massless when the contrast of the front in the contrast of the front in the contrast of the front in many regards, including the development in regulies of a stout plants.

ing from the girdle, however, are differently named in the two cases, for while it is probable that the iliac head of reptiles, termed the *iliotibialis*, is the same as the rectus femoris of mammals, it is far from sure that the ambiens of reptiles is the same as the sartorius, the "tailor's muscle" of mammals.

Two other dorsal muscles arising from the reptile ilium are none too readily comparable with mammalian muscles arising in this region. We have noted that in mammals there has been a major shift in posture of the thigh, and in consequence it is reasonable to expect changes in the related musculature. In reptiles an iliojenomist runs from the likae blade directly outward to the femur, in mammals a series of powerful gluteal muscles lies in much the same position, but differs considerably in its course and function in limb movement—particularly the deeper gluteals, which exert a powerful leverage on the femur in pulling the knee back or, conversely, pushing the body upward and forward on the leg. In reptiles there is a long itiofbalaris muscle running (as the name implies) from ilium to fibula. There is no such muscle in mammals; possibly it is represented by a long member of the gluteal series.

Beyond the knee, the extensor muscles of the pelvic limb show a pattern in both reptiles and mammals essentially comparable to that of the pectoral appendage.

VENTRAL MUSCLES (Figs. 187, 188, B, C, E, F). The ventral muscles of the hip and thigh region mainly adduct the femur and flex the knee joint; in locomotion, that is, they raise the body off the ground and push it forward. They are hence large, important and complex. They are disposed in three main groups:

- 1. A large deep muscle arising fleshily from much of the outer surface of the pubis and ischium (the fenestration of these elements is related to this muscle attachment). This has in replies the noble name of publischiofemoralis externus; in mammals it is the obtarator externus, with the quadratus femoris as a split-off fraction.
- 2. Covering the under surface of the thigh is a large and complex group of long muscles which flex the tibia. In reptiles these are the puboischiolibialis, flexor tibialis externus, flexor tibialis internus and puboishialis (more lovely names!); their mammalian homologues appear to be the gracilis, semimembranosus, semitendinosus and hicega.
- 3. In typical reptiles, powerful ventral limb muscles, the two caudifemorales (long and short), arise from the tail vertebrae and run forward to insert by tendons onto the femur, to which they give a powerful backward pull with consequent contribution to forward motion. In mammals, however, with reduction of the tail and changed limb posture, this group of muscles has been reduced to small and variable slips, such as the pyriformis.

The long ventral muscles of the "calf" are mostly concentrated into a powerful gastrocnemius muscle in all tetrapods. As in the case of the front leg

### (Fig. 188 continued)

flexur running down either side and the development of a powerful two-beaded "cull" muscle, the gartroenemius. In ammais the cull musculature has (except for the plantirs) changed to any attachment on the "bed bone." The long flexur of the digits, however, runs on the reduced planting the From this extend, as in reptile, sidine thendous and toe makes (an f. He superficial muscle of this set have been removed to show the deeper tendous and muscles), In both reptile and mammal there are, on the flexur surface, deep, short the muscles not show in the figures.

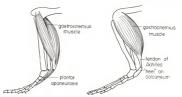


Fig. 189. Side views of the hind leg of a limred  $l(\vec{p})$  and a typical nammal  $(r(\vec{p},\vec{p}))$  to above the count test in action of the main call muscle, the gastencemism, in crienting the foot, in lower temporal in rounds the ankle region to act on the under surface of the foot by attending to a sheet of connective time, the plantar aponeurousis, which in turn makes connections with the toos ( $\vec{r}, \vec{p}_1$  (188,  $\vec{p}_2$ ),  $\vec{r}_1$  in mammals its action is simplified by the development of a heel on the calenaeum (of. Fig. 188,  $\vec{p}_2$ ), attachment of the muscle tendon here raises the foot of the grounds.

flexors, the problem of "rounding the turn" at the ankle is a major structural problem. Reptiles generally have solved this, as in the case of the fore foot, by the development of an aponeurosis. In mammals, however, a new type of footraising device has been evolved by the leverage of calf muscles inserting in a heel tuber of the calcaneum. The major gastroenemius heads no longer extend to the side of the foot, but insert by the "tendon of Achilles" onto this tubercle (Fig. 189).

### BRANCHIAL MUSCULATURE

Markedly different from the striated musculature so far considered is the branchial musculature, highly developed in the gill region of the ancestral vertebrates, and pensistently prominent in much modified form in even the highest groups. It is noted elsewhere that the skeleton and nerves of the pharryn are highly distinctive in nature. The pharyngeal musculature is equally noteworthy, for, in contrast to all other striated musculature, it arises, not from the myotomes but from mesenchyme derived from the pentomen of the lateral plate (Figs. 67, C. p. 104; 179, p. 204). The smooth musculature of the gut proper, posterior to the pharynx, arises in similar fashion.

Guf muscles, striated or smooth, are but anterior and posterior parts of a single great visceral system of muscles whose primary locus is in the walls of the digestive tract. For the digestive processes of stomach and intestine, the slow movement of smooth musculature suffices; for the vigorous movements needed in the pharynx of primitive vertebrates—for breathing and, still more primitively, food straining—striated muscle is needed. Generally the boundary, along the gut tube, between striated and smooth muscle lies at the posterior end of the pharynx. But this is not a fixed point, and both in fishes, on the one hand, and in manmals on the other, striated visceral musculature may extend back into the esophagus. In higher vertebrates the pharynx is reduced in size and importance,

but the striated pharyngeal musculature is persistently prominent, for portions of it have assumed a variety of natures as facial and jaw muscles and even a fraction of the shoulder musculature.

Branchial musculature is well developed in cyclostomes, as sheets of muscle constricting the gill pouches and as specialized muscles operating the peculiar "tongue." The construction of the lamprey musculature is, however, quite unlike that of other vertebrate groups and will not be considered further here.

In the sharks (Fig. 191, A) the branchial muscles show a pattern which muscle econsidered basal to that of other gnathostomes. Anterior clements are, however, already specialized for operation of the jaws. We shall, hence, follow the history of the muscles connected with the typical gill arches from the sharks upward through the higher vertebrates before returning to consider the muscles farther forward in the region of the fish hyoid and mandibular arches.

Muscles of the Typical Gill Bars and Their Derivatives (Figs. 190, 191, 4). Behind the hyoid arch there are typically, in fishes, five gill slits with four intervening arches, each with its own proper musculature as well as its own skeletal bars. Even when, in the land vertebrates, the gills themselves have disappeared as landmarks, muscles derived from various parts of the gill system can be readily traced because of their innervation. The gill muscles are supplied by a special series of cranial nerves, numbers V, VII, IX and X (cf. pp. 382–385, and Fig. 375). The jaw arch is supplied by nerve V, the hyoid by nerve VII, the first typical gill bar is the territory of nerve IX, and the further gill bars are innervated by special branches of nerve X (which continues onward far down the gut).

Although there is frequently a fusion of muscle tissues above and below the gill openings, each typical shark gill has a characteristic series of muscle slips proper to it. The most prominent element is the superficial constrictor, a broad, thin sheet whose filters generally run vertically in the flap of skin extending outward in the gill septum. Above and below, most of the constrictor fibers terminate in sheets of fascia on the back and throat, but deeper slips may attach to the gill bars and may form separate interbranchial muscles.

In addition there are deeper muscles. The arch adductors run from epibranchials to ceratobranchials and tend to bend the two together; dorsal interarcual

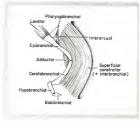


Fig. 190. A single gill arch of a shark and its musculature

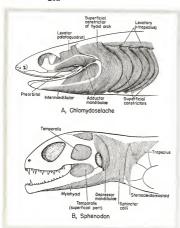


Fig. 191. Lateral views of the branchial arch musculature and its derivatives in a shark and the reptile, Sphenodon. (A after Allis; B after Adams and Fürbinger.)

muscles function similarly in connection with pharyngobranchials and epibranchials of the same or neighboring arches. Dorsally, fibers from the "neck" fascia run backward and downward to insert on successive gill bars as arch levens, but in many sharks most or all of these fibers run farther back to insert on the shoulder girdle.

In bony fishes the development of the gill musculature is more restricted.

sline gill septa are lost, the superficial constrictors are absent, although ventral
slips may persist as subarcual muscles; in teleosts the levators are lost and even
the remaining small muscles are reduced or absent.

Among tetrapods, gill-breathing larval amphihians retain a series of gill muscles resembling those of bony fishes, but in true land vertebrates the muscles moving the typical gill hars have disappeared except for small slips associated with the hyoid apparatus and laryns. There is, however, one conspicuous if aberant relic of the gill series in tetrapods— the trapezius musculature (Fig. 191, B). This is derived from slips of the levator musculature which, we have noted, and in sharks to run back above the gills to attach to the shoulder girdle. In land vertebrates these form a thin sheet of muscle which arises from the occipitde and back fascia and inserts along the anterior margin of the shoulder girdle.

Primitively this trapezius sheet attached to the clavicle and cleithrum, but with reduction or loss of these elements the attachment may be on the scapular front margin (or the corresponding spine in mammals) and may reach the sternum ventrally. Anterior and ventral slips may become separate muscles, such as the sternomastoid and cleidomastoid, and with reduction of the clavicle in many mammals may fuse with slips from the deltoid to form long slender compound muscles extending directly from head to front limb.

Muscles of the Hyoid Arch. Presumably in the ancestral jawless fishes muscles of the hyoid arch were comparable to those of typical gill arches. But in all living jawed vertebrates this arch, as we have seen, has become highly modified, and its muscles-which may be identified through their innervation by nerve VII-are modified as well. Even in sharks the only surviving muscle of the arch is the superficial constrictor. This muscle may be variously subdivided in fishes, however, with deep slips connecting hyoid arch elements with one another and with the jaw joint. Certain of these slips may persist as tiny elements in the hyoid and ear region of tetrapods; two slips, as noted below, achieve importance in land animals in connection with mouth opening.

In contrast with the trend to reduction of much of the hyoid musculature, the dorsal part of the hyoid constrictor sheet is persistently prominent. In bony fishes this constrictor is highly developed to control movements of the bony operculum covering the gill chamber. In land vertebrates, with loss of the operculum, this muscle spreads around the neck in a thin sheet, generally adherent to the skin, as the sphincter colli (Fig. 191, B). In mammals it expands in spectacular fashion to form the muscles of expression, discussed later (p. 221).

Mechanisms for mouth opening have apparently not been taken seriously (so to speak) by vertebrates (mouths tend, rather, to open by themselves), and various makeshift devices are seen in different groups. It was noted earlier in the chapter that ventral axial muscles run forward along the throat and may attach to the ventral portions of gill bars and jaws; a backward pull on these muscles is sometimes utilized in fishes for jaw opening. In most tetrapods except mammals there is substituted a depressor mandibulae (Fig. 191, B), an anterior slip of the hyoid constrictor which runs downward from the back of the skull behind the one-time spiracle (now the eardrum region) to attach to the back end of the lower jaw.

In mammals, as we have seen, the lower jaw has been refashioned; the elements about the region of attachment of the depressor muscle are lost, and the muscle with them. As a substitute, another slip of the hyoid muscle emerges to take part in the formation of a new jaw-opener, the digastric (Fig. 192, B). As its name implies, this has two bellies. The posterior one is a hyoid slip which runs downward from the ear region of the skull; the anterior belly is formed by fibers derived from the proper musculature of the jaws. The two may be at a sharp angle to one another, but between them successfully perform the none too arduous task of depressing the jaw.

Jaw Muscles (Figs. 191, 192). With the modification in gnathostomes of the elements of an anterior gill arch to form basic jaw structures, the muscles of this arch (innervated by nerve V) have become highly modified to serve special jaw functions. As seen in sharks, the jaw musculature consists of three parts: (1) The upper jaw in sharks is but loosely attached to the braincase; connecting these two skeletal elements, between eye and spiracle regions, is a levator palatoquadrati, rather comparable to the levator muscles of ordinary gill arches. (2)

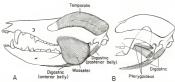


Fig. 192. Jaw musculature of the opossum. A, Superficial view; B, deeper dissection. The jaw is represented as transparent to show the pterygoid muscles, which attach to its inner surface.

The major muscle mass of the fish jaw segment is the addactor mandibulee, roughly comparable to the adductor of an ordinary gill, but of vastly greater size, since it performs the important function of pressing the jaws together in the biting or grinding motions essential to food intake. The main mass of the jaw adductor is arranged in simple fashion, running between palatoquadrate and mandibular cartilages. (A specialized preorbital muscle slip in sharks runs forward to aid in anchoring the jaws to the braincase.) (3) Unimportant is a ventral intermandibular muscle, a thin sheet of fibers connecting the two jaw rami and having fibers from the hyoid as well as the jaw muscle component.

In higher vertebrates the first and third of these components amount to little. The levator may persist as one or more slips in forms in which palate and braincase retain some degree of independent movement but is vestigial or lost in groups in which the skull is a solidly fused structure—chimacras, lungfishes, modern amphibians, turtles, croodiles, mammals. The ventral sheet between the jaws persists as a mylohyoid muscle and, as noted above, may contribute to the formation of the mammalian diesestric.

The adductor mandibulae and its derivatives remain prominent throughout the gnathostomes. In bony fishes and tetrapods the "cheek" region in which it lies is covered by dermal bones of the skull; in area of origin the adductor is not confined, as in sharks, to the upper jaw cartilage or the bones which replace it, but it spreads onto these dermal bones and may extend upward and inward to attach to the braincase as well. In lower tetrapods the adductor musculature is divided into two main groups: (1) temporalis and (2) pterygoideus. The temporalis muscle is the major component. In amniotes, as discussed in connection with the reptilian skull, fenestration of the skull roof allows greater freedom of action for the temporal musculature. In mammals the original temporalis is divided into two parts. The temporalis proper has much the original position of the muscle and inserts into the coronoid process of the mandible. A second muscle, the masseter, is more superficial in position. With its fibers running at a considerable angle to those of the temporalis, it pulls the jaw forward as well as upward; it is particularly highly developed in rodents. The little ptervgoideus muscles form a deep division of the adductor mass; they typically originate from the pterygoid region of the palate and insert on the inner or back surface of the jaw.

## SKIN MUSCULATURE

Although in tetrapods (in contrast to fishes) the skin usually lies relatively loosely over the surface of the trunk muscles, there are often applied to its understace thin sheets or ribbons of muscle derived from the underlying layers and functioning in skin movements. Such dermal musculature is little developed in amphibians and reptiles, except for slips derived from the pectoral muscles. In snakes, however, a dermal muscle is attached to each of the large scales, adding them in serving as holdfasts which prevent a backward slip in the undulatory motion. In birds dermal muscles are prominent in the skin of the wing.

The greatest development of dermal musculature is in mammals. In many forms almost the entire trunk and neck are enveloped in a continuous sheath of skin muscle, the panniculus cannosus (Fig. 193); the twitch of a horse's skin where a fly has settled is evidence of the presence and functioning of this muscle sheet. The trunk sheath of the panniculus is derived from underlying axial muscles, but in the neck the sphincter colli is, as we have noted, a part of the visceral musculature, innervated by the facial nerve (VII). In mammals this anterior part of the dermal musculature undergoes a striking development. Slips



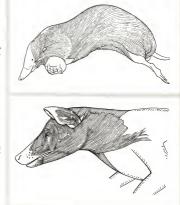


Fig. 194. Facial musculature; the head and neck of a dog. (After Huber.)

of the musculature associated with the facial nerve grow forward over the skull and on to the checks to form the facial muscles, or muscles of expression (Fig. 194), and are especially concentrated about the orbits, the outer car and lips

## ELECTRIC ORGANS

In several types of fishes, such as rays of the genus Torpedo, the electric "cell" Gymnotus and the electric catfish Malapterurus, there are developed special organs capable of producing a heavy electric shock. Weaker electric organs are present in a number of other fishes, and in some cases it seems clear that they are used as aids in navigation in much the fashion of radar. The bulk, at least, of these electric organs (Fig. 195) are modified muscular tissues. Muscles fibers are structures chemically adapted, as we have seen, for the rapid region of electricity rather than for muscular contraction.

The modified muscle fibers which appear to form the elements of the electric organs in most of these fashes develop as flattened plates of multinucleated protoplasm, each innervated by a nerve fiber, and arranged in series of piles, comparable to the old fashioned voltaic pile, famous in the history of electrical discovery. They form essentially an organic battery, made effective by plus and minus differences between the two surfaces of each plate. In the torpedo, strengths of more than 200 volts and 2000 wasts have been recorded.

Despite the usual basic similarity of their construction, the electric organs vary greatly in position and appearance in the different fish types. In the torpedo they are present as two large groups located on either side of the head in the expanded pectoral fins. The organ of the electric "ee" is formed from much of the tail musculature. In the electric caffsh of the Nile the electric dissue encired the whole body just beneath the skin; in this instance its origin from muscular tissue is not certain.

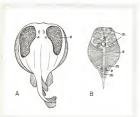


Fig. 195. Electric organs. A, The torpedo, a ray in which musculature of the expanded pectural fine has been transformed into electric cells (e). The skin is dissected away to show the electric organs. B, Section of the tail of the electric "cell" of South America (Gymnotus). Typical axial musculature (m) is present above and helow, but much of the tail muscle has been transformed into electricity, producing tissue (e). (A after Garten; B after the Busis-Revmodd.)

# 10

## BODY CAVITIES

In the vertebrates, as in all the more highly organized invertebrate types, most of the body organs are not bedded in solid tissues or mesenchyme, but are situated within the bounds of fluid-filled body cavities, more properly celomic cavities. The viscera are thus placed in a situation where they are more or less at liberty to move freely during their functional activity and to change the more readily in size or shape during growth. Before proceeding to the description of the organs which are enclosed in these cavities or border them, we may here give a brief resume of the arrangement.

Development of the Celom. The celomic cavities are formed in the mesodermal tissues and their linings are a mesodermal epithelium, the peritoneum. Something of their early embryologic development was noted in Chapter 5. In Amphioxus they are formed in the mesoderm in segmental fashion and are at first in direct contact with the gut cavity (Figs. 65, 66, p. 101). This condition (probably primitive) does not hold in true vertebrates; ephemeral cavities may appear in the somites or kidney-forming tissue, but permanent celomic cavities develop only in the lateral plate of the mesoderm and generally show no indication of a segmental arrangement. In forms developing from a mesolecithal type of egg the lateral plate at an early stage extends down the flanks of the body and the two sheets presently meet, or come close to meeting, in the ventral midline (Fig. 67, p. 104); in large-yolked types the lateral plates at first spread out widely to the sides (Fig. 62, p. 97), and only at a relatively late stage do the two sheets meet ventrally. At first each lateral plate is a solid sheet of tissue. Presently, however, it splits into inner and outer layers with an intervening liquid-filled cavity, the embryonic celom, continuous on either side for the length of the trunk; its outer and inner walls (apart from giving rise to connective tissues and other materials) are destined to form the parietal and splanchnic layers of the peritoneum (Fig. 196). The somatic peritoneum forms the inner surface of the great "external tube" of the body (the somatopleure of the embryo); the splanchnic peritoneum forms the outer wall of the gut tube and its outgrowths (the splanchnopleure).

As development proceeds the cavities of the two sides come to lie close to

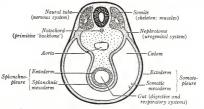


Fig. 196. Diagrammatic transverse section of a mammalian embryo to show the relations of the mesoderm. (From Arev.)

one another above and below the digestive tract (Figs. 2, B, D, p. 6; 200, B). They are separated only by this sheets of tissue, suspending the abdominal organs—the darsal mesentery above, a central mesentery below. The former is a persistent structure; the latter generally disappears for most of its length by the time the adult stage is reached. On either side, the celomic cavity, in the embryo, at least, extends far forward ventrally (Fig. 197, A) to reach the floor of the pharyn; (the development of gill pouches prevents its dorsal development for pharyn; the cavities or the exterior. However, the funnels of the oviduots open from them; in some lower vertebrates some anterior kidney tubules may tap the celom; a pair of small pores open to the surface from the celom in most fishes except teleosts.

The celomic structure of an early embryo is simple and readily understood; that of the adult is not. It is complicated, owing to three factors: (1) a pushing into the celomic spaces of other organs than those of the disceive tract—heart.

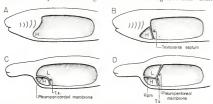


Fig. 197. Diagrammatic longitudinal sections of the body to show the evolution of the celonic cavity. A. A primitive condition, with the entire celons forming a single cavity. B. Typical fish condition; the pericardial chamber is separated from the main cavity. C. Typical amphiban and reptilian condition; the lungs are developed but the spaces in which they lie are in continuity with the main celons. D. Mammalian condition, with a formed displayment. H. Heart, L. Jungs.

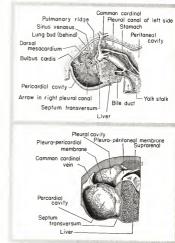
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gonads, kidneys, lungs: (2) longitudinal subdivision into compartments (Fig. 197)— —in most cases into a heart cavity and general body cavity, but with further subdivision in mammals and birds; (3) elaboration and twisting of the gut and outgrowth of gut appendages—liver, pancreas—with a consequent complicated folding of "mesenteries."

Pericardial Carity. The heart in all vertebrates becomes situated in the most anterior and ventral region of the embryonic celom, primitively in the floor of the "throat" below the gill region. At an early stage in development there forms behind it a vertical transcerse septum, separating this cavity from the celom of the trunk (Figs. 197, At 196, 199). This septum becomes a complete partition in most vertebrates, but a communicating opening persists in many fishes, notably sharks and hagfshes. The septum is utilized by the liver, which, as it grows, at taches to its posterior surface; this attachment persists in the adult, although in many cases the attachment is restricted to a relatively narrow ligament. The upper wall of the pericardial cavity is in fishes the floor of the pharynx. When, in tetrapods, the hugars cury he area dorsal to the tetrapods, the pharynx is reduced in size, the lungs occupy the area dorsal to the

Fig. 198. Lateral view of a dissection of the trunk of a human embryo 3 mm. in length, showing pericardial eavity (heart removed), pleural, and peritoneal cavities, anterior end of the body to the left. The transverse septum, with the developing liver, has formed behind the heart, but all body cavities are in open communication (cf. Fig. 197 A. B). (After Arey.)





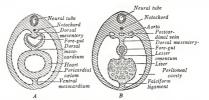


Fig. 200. Diagrammatic sections through the heart and liver regions of an amniote embryo to show the relations of the mesenteries. (From Arey, after Prentiss.)

heart, and a pleuropericardial membrane develops to separate the two organs (Figs. 197, C: 199).

General Body Carity. With the separation of the pericardial cavity, there remains in the majority of vertebrates a single great celonic cavity occupying, with its enclosed organs, most of the trunk region. The ventral mesentery, we have noted, tends to disappear for the most part; anteriorly, however, a portion of it, the lesser omentum, connects the stomach with the liver (morphologically ventral to the gul), and a falciform ligament may persist below the liver

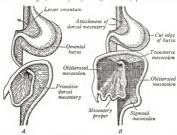


Fig. 201. Diagrammatic ventral views of the gat and mesenteries of a mammal in A. an embryo, and B. essentially adult conditions. 4 shows the general type of folding which the mesenteries must undergo because of the asymmetrical position of the stomach and twisting of the intestine. As shown in R. this folding may result in obliteration or risiss out parts of the mesentery. In 4 the bursa is a structure of mimer dimensions; in many mammals the relarged barsa sould cetted down, covering over much of the grade of the contraction of the state of the contraction of the right state (replace from the contraction) is about the contraction of the right the cut attachment of the leaver omenium to the liver. For lateral views of the same structures, see Fig. we 204, (From Arry.)

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(Fig. 200, B). The dorsal mesentery remains a continuous structure in mammals and reptiles, but tends to be broken into segments with intervening gaps in other groups. Distinct names are often applied to parts of the mesentery which connect with one organ or another; prominent is the greater omentum supporting the stomach. In teleosts and tetrapods the coiling of the intestine results in a confusing folding of the attached mesenteries (Figs. 201, 204). With the generally sigmoid curvature of the stomach is associated a folding of the greater omentum in such fashion that part of the right celomic cavity may come to lie in a pouch above and to the left of the stomach—the omental bursa.

Lung Pockets. When lungs are developed they push backward into the body cavity above the heart and on either side of the esophagus, here, in lung-lishes and lower tetrapods, they are supported by folds of tissue forming little mesenteries of their own (Fig. 202). It is of interest in connection with the development of the circulatory system that the right pulmonary fold, which ventrally touches the liver, has been utilized in lungfishes and tetrapods in the formation of the posterior vena caxa, which plunges down through this fold in its course toward the heart (cf. p. 330). In fishes, amphibians and many reptiles the lung cavities are merely anterior parts of the general celom and in some reputies the lungs may be more or less buried in the body wall, in other reptiles, however, the lung pockets may be closed off as separate pleural cavities, much as in birds and mammals.

The Celom in Birds and Mammals. The great development of air sacs in connection with the lungs in birds is associated with a complicated subdivision of the body cavity (Fig. 203). The original abdominal cavity is divided into a pair of lung cavities and two pairs of cavities surrounding the abdominal viscera; air sacs develop between lung cavities above and the sets of abdominal cavities below.

Fig. 202. Digrammatic cross section, looking forward, through the body of a lizard in the region of the lungs, to show the pulmonary folds, between which and the coopbagos lie pulmonary recesses. The left pulmonary fold is little developed; it is down the right fold that the posterior vena cava makes its way from the region of the posterior cardinal vein to the liver (cf. p. 330). (After Goodrich.)

Fig. 203. Diagram of transverse section through the thorax of a bird to show especially the subdivision of the celomic cavity. In addition to the pericardial cavity, the pleural cavities and the sacs dorsal and ventral to the liver are shown; the main intestinal celom is too far posterior to be included in this section. The thoraxic air sacs (hatched) are also present in section. (Mgr Goodrich.)





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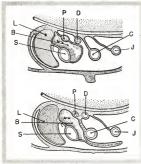


Fig. 204. Diagrams of embryonic and adult conditions of the omentum and bursa in a mammal; longitudinal sections, seen from the left side, with head end at left. In the embryo-(upper figure) the bursa is small; the entrance (epiploic foramen) is indicated by an arrow. In the adult of many mammals (lower figure) the dorsal mesentery, as the greater omentum, has become a long fold. The diagrams further show how the mesenteries of the gut may be fused together (as is here that of the transverse colon to the greater omentum), or obliterated (as is that of the duodenum, in the diagram): B, omental bursa; C, transverse colon; D, duodenum; J, jejunum; L, liver; P, pancreas; S. stomach. For comparable ventral views, see Figure 201. (After Arey.)

In mammals no air sacs are present, but the arrangement of celonic cavities is nevertheless complicated. The omental bursa is generally well developed as a large and nearly closed pouch (Figs. 201, 204), and the greater omentum may extend down from it ventrally as a great apron over the abdominal viscera. Further, as in birds and some repitles, the lungs are enclosed in separate pleural cavities which are closed off from the rest of the celon by the development of the daphragm (Figs. 197, D, 199, 205). The transverse septum, separating heart from abdominal cavity, is the principal ventral component of this complex structure. Above this, folds from the body wall extend inward on either side of the body, and are continued medially by the pleuroperitoneal membranes. These lateral growths meet folds growing out from either side of the mesentery which complete the diaphragm as a solid wall of tissue separating the abdomen from the chest. Into the diaphragm grow muscles from the axial system, so that it becomes a positive element in expansion and contraction of the lung cavities and is important in mammalian breathing.



Fig. 205. Anterior view of the disphragm region of an embryonic mammal, to show the various elements which make up the disphragm. Heart and lungs have been removed to show the posterior walls of the pleural and pericardial chambers. At this stage (as in the comparable Figure 241, p. 256) the pericardial cavity still extended to the ventral wall of the chest, whereas in the later stage of Figure 242. B, (p. 256) the penul cavities extend below it. (After Brounn, Goodriel Brounn, etc.)

## 11

## MOUTH, PHARYNX, RESPIRATORY ORGANS

The digestive tract, with its various outgrowths and accessory structures, looms large in both bulk and importance in body organization. In the present chapter we shall consider the mouth and pharyngeal region, "introductory" sections of the tract. These play little role in alimentation beyond the reception of food, but are highly important in other regards—motably as the place of origin of respiratory organs and of important glandular structures.

## THE MOUTH

From the mammalian or human point of view the mouth appears to be a well-defined structural unit, with fixed, uniform features such as the lips, tooth row, tongue, and salivary glands. But a broad survey of vertebrates shows that mouth structures vary widely, every one of the familiar landmarks may be absent in one group or another. Except that it is an inturned area—a buccal eavity—leading to the pharynx, we can make few statements about the mouth that will hold true for all vertebrates.

The embryonic gut cavity of vertebrates, the archeateron, was long ago recognized as comparable to the adult digestive cavity of coelenterates and a number of other simple invertebrate types; into this cavity there is but a single opening, to which the vertebrate embryonic blastopore and adult anus are broadly comparable. In the more highly organized invertebrate phyla, however, a mouth develops at the opposite end of the gut as a progressive feature. That vertebrates followed a similar evolutionary course is suggested by the ontogenetic history. In the embryo the archeateron ends blindly at its anterior end, the region of the future pharynx (Figs. 206. A, 248, p. 261). In front of this area the head turns



Fig. 206. 4. Diagram of a larval amphiblian (at about the stage of Fig. 70, £), in longitudinal section, to show the cutest of the endodern displayed, and it reducins to structures of the mouth region. B. Diagram to show the comparative position of the menth margins in various types of vereleases (cf. test). downward over the surface of the vyolk-swollen body or yolk sac, producing be neath it an inturned fold or pocket of ectodorm, the stomodeum. This is the primitive mouth cavity, at first separated by a membrane from the adjacent pharynx. Later the membrane breaks down, mouth and pharynx are placed in continuity and the gut has thus acquired an anterior opening. The cpithelia of the two regions concerned blend with one another and in later stages are difficult or impossible to distinguish; broadly, however, the pharynx continues to be lined, mainly if not entirely, with endoderm, but the mouth epithelium, in contrast, is ectodermal, essentially a continuation of the skin epidermis.

The extent of the mouth cavity in the vertebrate groups is highly variable (Fig. 206, B). One would, a priori, expect that the mouth of the adult would include in general the same stomodeal area in all groups. But this is far from the

Two good landmarks are always present in the roof of the embryonic stomodeal region. Near the outer end of this funnel, beneath the swelling forseronic in the swelling former and the swelling former and the swelling former and the swelling former and the swelling former than the swelling former and the swelling former and the swelling former and the swelling former and the swelling form much of the adult pituitary body. In most sarcopterygians and all terrapods the jaw margins form a bridge beneath the nasal pockets, so that internal as well as external openings are present, and the site of the hypophyseal pouch lies far back of this point; the mouth cavity is extensive. In ray-finned fishes and sharklike forms, however, the nasal sacs are external to the jaw margins; the mouth is, hence, less developed in these groups. Still less inclusive is the peculiar cyclostome mouth; embryonic development shows that it corresponds only with the inner recesses of the mouth cavity of the higher vertebrates. In the larval evelostome (Fig. 207) nasal pit and a hypophyseal pouch are found in the larval evelostome (Fig. 207) nasal pit and a hypophyseal pouch are found in the



Fig. 207. Section of the head of a larval lamprey. At this stage nasal and hypophysical sacs are still ventral in position (cf. Fig. 231, p. 247).

stomodeal depression, somewhat as in other vertebrates. But as the embryo develops, forces of differential growth cause a rotation of both nostril and pit (the two are closely connected) forward and upward on to the outer surface of the head, as in the hagfish (Fig. 17, p. 37) and, in the lamprey, to a position high on the dorsal surface, far removed from the adult mouth (Fig. 231, p. 2447). Most of the outer surface of the lamprey head is thus covered by ectoderm which in gnathostomes lies within the mouth.

ln a majority of vertebrates the mouth margins are formed by lips, soft pliable skin structures. In cyclostomes the mouth opening is rounded (as the group names implies); the "lips" bear sensory; tentacles in hagfishes, and in lampreys form an effective sucker by which the animal attaches itself to its prey (Fig. 231, p. 247). In many other vertebrate groups the lips are small and unimportal skin folds, and in such forms as birds, turtles and a few mammals are converted into a bill or beak which functionally replaces a reduced or absent dentition. In mammals, in general, the lips are, on the contrary, highly developed; they are separated by deep elefts from the jaw margins and rendered mobile by the presence of the facial musculature. The mouth opening generally terminates in manmals well forward of the jaw articulation, and there is thus created a skin-covered check region, which, in such forms as Old World monkeys and rodents, may expand into pouches useful in the carriage of food.

In the mouth roof, the palate, of the typical crossopterygians and tetrapods there develop paired choannae, the internal openings of the nasal passages. In amphibians the mouth roof is nearly flat; in reptiles, however, the roof is vaulted, giving an improved passage for air back from the internal nares to the pharyax and lungs. In crocodilians and mammals (Figs. 166, C, p. 189; 167, p. 190; 208, 209) this air channel has been shut off from the mouth by the secondary palate noted in our discussion of the skull; this "hard palate" is extended backward in mammals by a thick membrane, the soft palate (Figs. 208, 209). The vomeronasal organs (p. 346) may gain openings to the mouth roof independently of the choanae in some reptiles and mammals. In modern amphibians the tissues of the palate (and of the mouth cavity in general) are richly vascularized and the mouth functions as an important breathing organ. In mammals there are often cornified transverse ridges on the palate which aid in the manipulation of food. In the toothless whaleloone whales (Mysticcii) these have

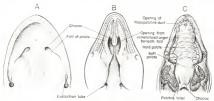


Fig. 208. The roof of the mouth in A, a wrodele; B, a lizard; and C, a mammal (dog); to show particularly the position of the choanae.



Fig. 209. Median section of the head and neck of a rhesus monkey. (After Geist.)

developed into long parallel plates of "whalebone" hanging down into the mouth cavity; fringes on their margins pick up small marine organisms which are licked off by the tongue and form the food supply of these giant mammals.

In fishes the lower ends of the gill hars, with accompanying musculature, slant forward below and between the jaws into the floor of the mouth. In cyclostomes, derivatives of these structures form an extrusible structure armed with norny "teeth" wherewith to rasp the flesh of the animal's prey. This is called a tongue, but it is obviously not homologous with one, and in fishes generally there is little in the way of a true tongue. This organ is essentially a development in tetrapods for the better manipulation of food in the absence of water; reduction of gill function enables land animals to put to this new use the gill bars and their musculature. The tongue musculature, we have noted, is derived from the hypobranchial system, and the tongue is anchored at its base by modified gill bars—the hyoid apparatus.

There are numerous specializations in tongue structure among tetrapods. Thus, while some anurans are tongueless, common frog and toad types have a tongue readily protrusible to pick up an insect with its sticky tip; chameleous have a comparable structure; woodpeckers and several mammal termite-eater; have very elongate tongues. Mechanisms for tongue extrusion are varied cases of rapid extrusion, muscular action is always involved, but modest expansion or extrusion may be due to filing blood sinuses of lymph sac.

Apart from a specialized gland in the lamprey, which prevents coagulation of the blood of its prey, fishes generally have little in the way of mouth glands except scattered mucous cells. In land vertebrates, in the absence of a water medium, saltivary glands make their appearance as aids in moistening and swallowing food, secreting mucin and a more watery material to produce the salvia. In amphibiians, reptiles and birds such glands are usually small, if sometimes numerous. In amphibians, however, there is generally a large median internatillary gland in the anterior part of the palate, and in many snakes and in the Gila monster (the one poisonous lizard) there develop special mouth glands which produce toxic venoms which pass by way of a groove or duct in adjacent fangs into the flesh of the victim. In mammals salivary glands are highly developed, notably as prominent paroxid, submaxillary and sublingual glands. For the most part salivary glands lack chemically active materials; but in many mammals (including man), many birds, and even a few anurans, an enzyme—ptyalin—may be present as an advance guard of the enzyme army which was originally confined to more posterior regions of the alimentary canal.

## DENTITION

The teeth, although modified parts of the dermal skeletal materials, may be appropriately discussed here as "inhabitants" of the oral cavity. They are unknown in lower chordates and in javless vertebrates, living or fossil, although cyclostomes have functionally comparable horny structures which may be degenerate denticles. With the advent of javs, it seems, teeth simultaneously developed as biting structures; by the broader feeding possibilities opened out by these new devices the way was paved for the rise of the gnathostome vertebrates to their present estate.

Tooth Structure and Position. In their simplest form (Fig. 210) teeth are contical structures of the type seen in many fishes and reptiles and in the anterior part of the mammalian dental hattery. Frequently, however, more complex types appear, notably teeth in which the upper surface is more or less broadened to form a cronn for chewing or crushing purposes. In the tooth interior is a pulp cavity, with soft materials including blood vessels and nerves. At the base may be present one or more roots by which the tooth may be firmly implanted in the jaw.

The major tooth materials are enamel and dentine. Enamel, as found in mannal teeth, is exceptionally hard and shiny in appearance and forms a thin layer over the tooth surface; in some lower vertebrates enamel appears not to develop, but is replaced functionally by an exceptionally hard outer layer of dentine. This latter substance forms the bulk of the tooth. It is essentially similar in chemical composition to bone, but differs structurally in that the associated cells have their bodies in the pulp cavity and send out long straight processes into the den-

Fig. 210. Sections through a mammalian incisor, A, and molar, B. (After Weber.)





Fig. 211. Diagrammatic sections through reptilian lower jaws to show the distinction between thecodont, A, pleurodont, B, and acrodont, C, tooth attachments.

tine through numerous fine parallel tubules—canalicali. In sharks, in the absence of bony jaws, the teeth are attached by fibrous connective tissue; fibrous attachments are also characteristic of snakes and some lizards, and ligamentous attachments may be found in teleosts. In general, however, teeth are firmly attached to the underlying bony elements, often by a spongy bonelike material, cement. Most commonly the teeth are inserted in sockets—the theodona condition (Fig. 211); in other cases (as in Sphenodon and most teleosts) they may be fused to the bone surface—the aerodona type; in many lizards a variant is the pleurodona condition, where the tooth is attached by one side to the inner surface of the jaw bones.

The most important element of the vertebrate dental equipment is a marginal row of tech along each upper and lower jaw. Such teeth, although sometimes reduced or absent, are to be found in representatives of every class of jawed vertebrates. Teeth are not, however, confined to the jaw edges; teeth or denticles may develop from the ectoderm at any point, and since the mouth is lined with ectoderm, it is not astonishing that in many groups of vertebrates (barring birds and mammals) teeth are present on the dermal bones of the palate (cf. Figs. 151, B, p. 177; 152, D, p. 178), and are to be found on the inner surfaces of the lower jaws in bony fishes and extinct amphibians; in actinopterygians teeth may even develop in the pharynx, into which the ectoderm appears to extend in this group.

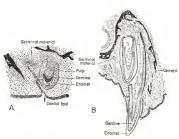


Fig. 21.2. Two sections of a crocodilian upper paw to show tooth development in lower tetrapods. A. Embryo with a first tooth developing and gernainal material in reserve at the base of the dental fold. B. Mature animal; a tooth is functioning, but is being resorted at the inner side of the rost, where the next successional tooth is already in process of formation. Germinal material for successional tech persists. (After Röse.)

It has long been recognized that teeth and the dermal denticles of the shark skin (cf. Fig. 97, p. 133; 216) are essentially similar structures, derived from ectoderm and underlying dermis, and hence are presumably homologous. It was once believed that teeth originated directly from discrete dermal denticles which lay along the mouth margins. Our current conceptions of the nature of the primitive fish as having a bony skeleton demands a modification of this idea. Shark denticles, as we have seen, appear to represent surface tubercles on the bony plates of ancestral fishes, the remaining layers having, so to speak, melted away during the course of evolutionary history. Teeth, we believe, similarly represent such dermal tubercles which lay on the surface of plates situated at the jaw margins. We may thus continue to regard teeth and dermal denticles as homologous, for although they have not descended one from the other, both trace back to a common ancestry as superficial "ornaments" on the dermal bony plates of ancestral vertebrates.

Tooth Development and Replacement. Embryologically, only the enamel is an ectodermal product, the remainder of the tooth mesodermal in origin. The first embryologic indication of tooth formation is an infolding of the epidermis. In marginal tooth rows, there develops as a continuous furrow the length of the jaw, a dentinal lamina, from which individual tooth germs develop (Fig. 212). If, as is usually the case, a succession of teeth is to develop, the germinal material is not used directly, but, while remaining deep within the jaw, buds off a bit of tissue which gradually moves toward the surface. These tooth buds, thus of ectodermal origin, usually form as hollow cones which outline the future surface of the tooth. The bud typically secretes the enamel of the tooth on its inner surface, hence the name enamel organ frequently applied to it. Meanwhile cells of mesenchyme origin gather within the cavity of the enamel organ; they deposit the dentine of the tooth, but their cell bodies remain in a persistent pulp cavity, with which small blood vessels and nerves come to be associated. As growth takes place, the tooth works toward the surface and finally erupts; meanwhile one or more successional buds may have formed from the germinal material and pushed outward for replacement.

In mammals (as we are well aware) there is no tooth replacement, apart from the succession of "permanent" teeth for a "milk dentition" in the front of the mouth. Far different is the situation in most other vertebrates. Little is known of the replacement of teeth found on the palate and inside of the jaw in many bony fishes, amphibians, and reptiles appear to undergo little if any replacement. But as regards the major, marginal dentition of fishes, amphibians, and reptiles, it is clear that tooth replacement continues through life. Teeth are constantly being formed deep within the tissues of the jaws; they grow in size, crupt, and function and presently, through resorption at their bases or loosening of their connections with the jaw elements, are shed and replaced by a new tooth "generation."

In many fishes, amphibians, and reptiles the tooth row has a seemingly irregular appearance with old teeth, mature teeth, and newly crupted teeth scattered along the jaw in apparently random fashion (Fig. 213). Actually there is method in this seeming madness. Replacement is taking place in an interesting way, which guarantees a continuous function of the dentition despite frequent renewal of individual teeth. The teeth and tooth germs give the impression of being arranged in two series, the "olds" and "evens" in each tooth row. One may find a condition in which, for example, in a given area of the jaw, the odd-numbered teeth

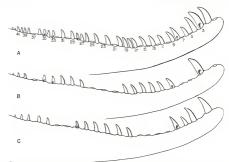


Fig. 213. Inner surface of the lower jaw of a primitive fosuil reptile (Ophiacodon) to show the alternation in tooth replacement between odd and even tooth series. The gaps in the tooth row seem haphazed at first sight; bowever, if the two series be considered separately, as in B and C, it will be seen that each includes several waves of replacement arranged in a regular alternating manner. (Certain tech —3, 8, 28, 33, 35—show recuprison at the root and are at the point of being [out.)

are functional; between them, in place of the even-numbered ones, are socked within which new teeth are in process of formation. Later this region may show a condition in which both sets of teeth are in place at the same time, but the odd set shows evidence of age and wear. A bit later still, the odd-numbered teeth drop out, leaving the even series, the functional set, and so on. This neat device guarantees that at least half the teeth in any region will be functioning at any time. The situation is complicated by the fact that replacement appears to take place in waves that travel along the jaw ramu; at a given time the "even" set may be functioning in some areas of the jaw ramus, the "odd" set in others.

This type of tooth replacement appears to be due to waves of stimulation that proceed, one after another, from the front of the tooth row along strands of tissue connecting the series of tooth germs; the alternating appearance of "odds" and "evens" is due to the spacing between successive waves.

The probable situation is that shown in Figure 214. In a and b, the horizontal lines represent the persistent strand of tissue connecting successive tooth germs in many vertebrates, the vertical lines the distance from the level of the tooth germs up to the surface of the jaw. In aI it is assumed that an impulse for tooth formation has begun at the most anterior germ position, and a tooth radiment (or "anlage," represented diagrammatically by a black dot) has formed. In a2 the impulse has travelled to the next position and started a second rudiment; meanwhile the first embryonic tooth in position one (represented by a small circle) has grown somewhat and moved up a bit toward the mouth surface. The stimulus continues to travel backward, initiating tooth development at successive

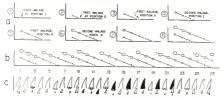


Fig. 214. Diagrams (discussed in the text) to show the mode of tooth replacement in typical lower vertebrates. (After Edmund.)

positions until, in the diagram at a8, this first stimulus has produced a row of teeth of which the first (represented by a large circle) has reached maturity. But meanwhile a second stimulus, spaced somewhat more than two tooth germs behind the first, has followed, and a third has just made its appearance.

If this sequence be continued, the mature jaw will obviously come to have the structure diagrammatically shown in b, and as seen in side view, in c. Here there is, at first sight, a seeming jumble of old, mature, and young teeth and tooth germs of various sizes; but, as we have just seen, the underlying principle is a simple and orderly one. In c one series of alternate teeth is shown in black; we see here an alternation between black and white teeth—between "weres" and "odds"—quite similar to the alternation found in the actual jaw of Figure 213. If the spacing between impulses had been exactly two tooth germ intervals, there would be an exact alternation of odd and even series the length of the jaw. But if the interval is somewhat greater than two tooth spaces (as in the example shown) or somewhat less, the appearance will be seemingly irregular but basically or-derly.

Teeth in Lower Vertebrates. No teeth are present in lower chordates or fossil ostracoderms, most of which are-or were-food strainers, nor in cyclostomes (where the rasping "tongue" is armed with horny, tooth-like structures). In all jawed vertebrates, however, teeth are universally present except where secondarily lost, as in turtles and modern birds. The most generalized type of tooth is that of a simple cone, present in a majority of elasmobranchs although often modified by accessory cusps or by flattening to give a triangular shape. In some sharks and most skates and rays the teeth may be flattened to form a crushing battery for feeding on molluses (Fig. 215). In chimaeras, likewise primarily shellfish eaters, the dentition is reduced to a pair of crushing plates in both upper and lower jaws and an accessory pair of small upper plates (Fig. 217, A). An analogous development is present in lungfishes (Fig. 217, B); the marginal teeth are lost, and the dentition typically consists of four fan-shaped compound dental plates (plus an accessory upper pair). Among actinopterygians the conical tooth shape is primary. In teleosts the cement-like material joining tooth and jaw bone may form a massive base for the tooth as essentially a separate "bone of attachment" (Fig. 218). In many instances large "fangs" are attached to the jaw by an elastic hinge, bending inward to allow the prey to enter the mouth but opposing 238 THE VERTEBRATE BODY



Fig. 21.5. The lower jaws of a primitive living shark, Heterodontus (Cestracion), the Port Jackies shark of the Pacific. The teeth differ greatly between front and back parts of the jaw. Rows of successional teeth are formed down within the inner surface of the jaws. (From Dean.)

its secape. In higher actinopterygians the maxilla becomes toothless, and in some teleoasts the marginal dentition disappears entirely; reliance is placed on palatal and pharyngeal teeth, often numerous. Many ancient crossopterygians were notable for the presence of longitudinal grooves on the teeth; these represent infoldings of the ensmed, often of complicated pattern, giving the tooth in cross section a labyrinthine appearance (Fig. 217, C. D). This crossopterygian tooth type is repeated in many of the oldest amphibians; it is so prominent a feature that it gives the name Labyrinthodontia to the ancestral amphibian group. In modern amphibians, living on small and soft materials, the teeth are small and simple in structure, and are entirely absent in some toads.

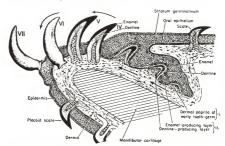


Fig. 216. Section through the paw of a shark, to show stages (I-VII) in the development of a tooth to its functional stage and to the point where it is about to be shed (VII). For comparison, placiod section, (denticles) in the adjacent epithelium are shown as well. (From Rand, The Chordates, The Blakiston Company.)

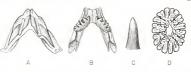


Fig. 217. 4. Dorsal view of the lower jays of a chimacra, to show the pair of large both plates, of complex shape, which cover most of their surface, B, Similar view of the bone of centents of the jac of the langths Epiceratodus, to show the pair of fan-shaped toothplates, C, External view of a growed a lookyhelike their characteristic of crossoperegrains and ancestral tetropole. D, Section through a tooth to show the complicated folding of the enamed layer (heavy black line). (A after Deam; B after Watton; C and D after Bustrow).

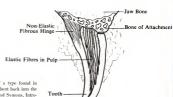


Fig. 218. Section through a tooth of a type found in many teleosts, in which the tooth may be bent back into the mouth on a fibrous hinge. (From Scott and Symons, Introduction to Dental Anatomy, The Williams and Wilkins Co.)

In a majority of reptiles the teeth are essentially of the simple conical type. Palast letch were present in ancestral reptiles and are preserved in Sphenodon, snakes, and lizards, such teeth are absent in crocoditians. Turtles have lost their teeth, relying instead on a horny bill. Ancestral reptiles generally had teeth inserted in shallow sockets, and typical thecodont teeth are seen in crocodiles. Most lizards, however, have a pleurodont type of tooth attachment, and some lizards (including chameleons) are acrodont, as is Sphenodon; in snakes the teeth are attached only by fibrous tissue. The primitive bird Archaeopteryx was toothed, but the bill (plus gizzard stones) has functionally replaced the dentition in later birds.

In the fossil mammal-like reptiles are seen stages in the initiation of the mammalian type of dentition. The most ancient members of this series, the pelycosaurs, show the development of large upper stabbing teeth comparable to mammalian canines, separating incisors anteriorly from a series of cheek teeth (Fig. 164, A, p, 187); various therapsids show further stages in the evolution of a mammal-like dentition (Fig. 164, B, C).

The Mammalian Dentition. The most primitive of living mammals, the monotremes, are aberrant in having entirely lost their teeth as adults, and reduc-



Fig. 219. Left side view of the dentition of a generalized placental mammal, showing permanent dentition in A; B, deciduous teeth. dc, Deciduous canine; di, deciduous incisors; dm, "milk molars" (= deciduous premolars).

tion or loss of teeth is found in various other forms, notably antesters and whalebone whales. Typically, however, mammals have a short marginal series of teeth in each jaw half, in which four tooth types can be distinguished in anteroposterior order (Fig. 219, 4). Most anterior are incisors, nipping teeth with a simple conical or chisel-like build; next a single conine, primitively a long, sharp stabbing structure. Following the canine is a series of cheek teeth, in which there tends to develop a grinding surface on the crown; the more anterior cheek teeth are the premolars; the posterior ones, the molars, are distinguished by the fact that they premolars are the posterior ones, the molars, are distinguished by the fact that they have no "milk" predecessors in the young and, further, are generally larger and have a better developed crown than the premolars. In early fossil mammals the number of teeth in the various categories appears to have been variable and rather high; primitive placentals, however, settled down to a count in each half of each jaw of three incisors, a canine, four premolars and three molars.

There has been devised a simple "shorthand" for the nomenclature of placental molar teeth and for the number of teeth of each type present in a given mammal. The letters I, C, P and M followed by a number in upper or lower position will define any tooth in terms of the original placental formula: I', for example, refers to the most anterior upper incisor, M<sub>s</sub>, the last lower molar. The number of teeth of each type present, above and below, in the dental equipment

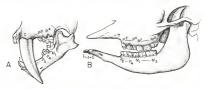


Fig. 220. Two specialized mammalian dental types. A. Felidi, E. the cow. (For the felid, the exinteaber-tooth, with criterine specialization, is abown, la the felidis the dentition is much reduced; there are modest incurs and source cannies (concealed in the figure) and stabiling upper cannie. In the check title remains except the currassistion [77]. In the ruminants the check terch are expanded into a granding battery; they are separated by a diastema from the cropping terth—here consisting only of lower incisions and canine, working against a showny also of the upper jace.

of any mammal, can be formulated in succinct fashion. The dental formula  $\frac{3.14.3}{3.14.3}$  indicates the presence of the primitive placental formula on either side of both upper and lover jaws (the number of incisors, canines, premolars and molars are represented by successive figures). The total number of teeth present in the mouth of such an animal is forty-four. The human formula is  $\frac{2.12.3}{2.12.3}$  i.e., we

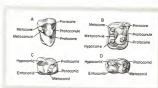
have lost an incisor and two premolars from each half of each jaw and reduced our teeth to a count of thirty-two.

Incisors are retained in most mammal groups, although the ruminants, for example, have lost the upper incisors and must crop grass by a bite between lower incisors and gums. The elephant's tusks are greatly enlarged upper incisors. In rodents a pair of upper and of lower incisors are developed as gnawing chisels which grow persistently at their rots as their tips are worn away. Canines are prominent in carnivores, and reach their maximum in the extinct saber-tooth "tigers" (Fig. 220, A); in nonpredaceous mammals they may be retained as defensive weapons or, in males, for use at mating time, but are generally reduced and often lost.

The cheek teeth have a varied history. In carnivores, in which there is little chewing of the food, they tend to be reduced in number and often in size, except that in most terrestrial carnivores a single pair on either side are specialized as shearing teeth—the carnassials (Fig. 220, A). In herbivores, on the other hand, the cheek teeth are usually retained (except for the frequent loss of the first premolar) and develop as an efficient grinding battery which is usually separated from the cropping teeth by a gap in the tooth row—a diasenta.

The crowns of the mammalian cheek teeth—particularly the molars—develop a varied and complicated pattern of cusps which are valuable in diagnosis of relationships and consequently have been studied in detail by systematists, paleontologists and anthropologists. Only the basic features of these molar patterns, as found in placental mammals, will be noted here (Figs. 221, 222). The nomenclature of the cusps is simple. Each is termed a cone; a small cusp is a conale; a lower jaw element has the sulfix—id. Typical cusp patterns and their nomenclature are illustrated in Figure 221. The early fossil history of the tooth patterns is incompletely known and some facts are in dispute, but in generalized primitive placentals the upper molars had a triangular shape, with three major cusps, one at an internal apex, two at the external base. It is believed that the lower teeth were originally similar triangles (but with internal bases and external apices) with a similar triof ocusps, with anness similar to those above. However,

Fig. 22.1. Diagrams of molar took patterns of placental mammals. In all cases, outer edge of tooth above, from dege to right. A. Right upper molar of a primitive form. B. The same of a primitive form. B. The same of a type in which the tooth has been "squared up" by addition of a hyperone of the back inner corner. Cli tower molar of a primitive form with two cusps. D. The same of a type in which the tooth has been "squared up" by the loss of the paraeonid.



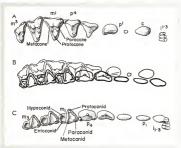


Fig. 222. Diagrams of the dentition of a primitive placental mammal (based on the Eocene in-sectivore Didelphodus). A. Crown view of right upper teeth; C. crown view of left lower teeth; between, in B., the teeth are placed in occlusion, the outlines of the lower teeth (heavy lines) superposed on those of the uppers. (After Cregory.)

such teeth, if meeting one another on closing of the jaws—occlusion—would tend to pass rather than meet one another. With resulting greater efficiency, each lower molar developed a "heel" will two additional cusps, into which fitted the apex of the triangular upper molar (as shown in Figure 222, B). This type of lower molar, already present in early placentals, is shown in Figure 221, C. A further pin molar development taken by many herbivores or mixed feeders is to "square up" both upper and lower grinders to oblongs, as shown in Figure 221, B, D. As can be seen, this is accomplished in the upper teeth by adding a fourth major cusp at the back inner corner and in the lower by losing one of the original three; in either case their results a tooth with four major cusps.

The cusps were primitively sharp-pointed; this, however, is ineffective for chewing purposes. In mixed feeders (such as men and swine) they tend to be rounded "hillocks"—the bunodont type. In many ungulates the cusps may connect to form ridges, the lophodont condition, or the individual cusps may assume a crescentic outline in a selendodont pattern (Fig. 223).

Grazing presents a serious "problem" to an ungulate, for grass is a hard, gritty material which would wear a low-crowned tooth to the roots in short order.



Fig. 223. Crown views of molar tech of A, thinocrose, B, honce; C, ox; to show types of molar patterns. The white areas are worn surfaces showing dentine; the black line surrounding the white is the worn edge of the enamet, stippled areas, consent covering or unworn surface. At is a simple liphoton type, with an external ridge dabovel and two cross ridges; the development of this pattern by connecting up the cusps seen in Figure 221. B, each ne readily followord. The torse (B) shows a development of the same pattern into a more complex form in which the primitive lophodont pattern is obscured. C shows a eleudooth pattern characteristic of the runimants; each of four minar cusps ackses on a crescentific

Fig. 224. Diagrams to show the development of a hypsodont tooth. A. Normal low-crowned tooth (cf. Fig. 210). B. Hypsodont tooth, with cusps elevated and the whole covered by ecment. As a tooth of this sort wears down to any level, such as that indicated at as, it will be seen that no less than nine successive layers of contrasting materials are present across the crows surface.

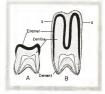




Fig. 22.5. Diagram to show the composition of the "permanent" dentition of a mammal; left upper teeth of a generalized placentall mammal. One complete set of teeth (f) develops from incisors back to modars. All of these except the modars, however, are shot (las indicated by stipple.) A second set of teeth develops (fi), but never produces modars. Hence the "permanent" dentition includes portions of two tools series (cf. Fig. 219).

In relation to this fact we find that such forms as horses and cattle have developed a high-crowned—hypsodont—tooth type (Fig. 224). One could, in imagination, develop a high-crowned tooth by elongation of the dentine-filled halls (of the tooth body, leaving the cusps in their original shape on the grinding surface. This actually occurred in some early fossil mammals, but has generally proved unsuccessful, for once the hard enamel surface of such a tooth is worn away, the bulk of the wear falls on the relatively soft dentine. Successful forms have hypsodont teeth built on quite another plan. The height is attained by a skyscraper-like growth of each cusp or ridge on the tooth; these slender peaks are fused together by a growth of cement over the entire tooth surface while it is yet beneath the gums. As wear takes place, it grinds down through a resistant complex of layers of all the tooth materials—enamel, dentine, and ecement.

#### CILLS

The pharynx is a short and unimportant segment of the digestive tract in the higher vertebrate classes—a minor connecting piece between mouth and esophagus where ventrally the glottis opens to the lung apparatus and dorsally the paired eastachian tubes lead to the middle ear cavities (Fig. 209, p. 232). In mammals it is merely the place where air and food channels cross one another in awkward fashion, and where there accumulate masses of lymphoid tissues, the townists. But from both phylogenetic and ontogenetic view points the pharynx is an area of the utmost importance; it is the region in which are developed the gill pouches, basic in the construction of respiratory devices in lower vertebrate classes, and persistently important in the developmental story in higher groups.

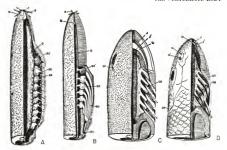


Fig. 226. Heads of various takes to show gill arrangement, J. The slimchag Bellelotonia, B. haghin Myxine, C. a shark: J. a telora. The right half of each is sectioned horizontally through the plaryax. Abbreviations: B, barbela around the mouth: BD, duets from gill pouches: BD, common outer openings of gill pouches: BS, gill sacks. EB's, seas sectioned to show internal folds of gill; G, gut (plaryax); GB, cut gill arch; GB, gill rakers; J, J', upper and lower javes; M, mouth; N, N', anterior and posterior openings of snast chamber; OP, operculaus; PS, princiee. (From Deurs)

In small animals with a permeable skin, sufficient oxygen can be readily obtained by exchange of gases through the skin. But in forms of greater size, in which the skin area may become insufficient to supply the need, and in forms with relatively impermeable skins, special respiratory structures—gills—are needed. These are formed in a variety of ways among invertebrates; in the vertebrates and their close chordate relatives, as we have seen, they take the form of internal gills—respiratory structures located in a series of slits or pockets leading from the pharyageal region to the surface of the body. As the locus of origin of these slits, the pharynx is a highly developed and highly important part of the digestive tube in the lower vertebrate classes.

The Gill System in Sharks. A characteristic development of the gill system is sen in sharks (Fig. 226, C.). On either side of the long pharynx a series of openings runs outward to the surface of the body. Anteriorly, there is generally present a small and specialized paired opening, the spiracle (described later); back of it, on either side, are found the typical gill slifs, five in number in most sharks (six or seven in a few special cases). In these slits are located the respiratory organs, the gills. Water, brought in through the mouth to the pharynx, flows outward through the gill slits; in its passage past the gill surfaces, the respiratory exchange takes place. The term gill arth\* is applied to the tissuel lying

<sup>•</sup> There is a source of confusion bere, for the term "arch" is often used in three different senses in connection with the gill region. As noted in Chapter 7, it may refer to the series of bars which form the skeleton of each gill segment. The word is also used to describe the arterial blood vessels—arotic arches —which traverse each gill (cf. Chapter 14). In the present chapter it is used in a broader, inclusive sense, to describe the total structure tring between two successive gill aller.





between successive openings. The region between mouth and spiracle is the mandibular arch; that between the spiracle and the first normal gill slit, the hyoid arch; more posterior gill arches are generally referred to by number.

Each gill arch includes a series of characteristic structures (Fig. 227, 4). We have earlier described the skeletal elements, including gill bar elements, gill rakers and gill rays. In addition there are branchial muscles, arch blood vessels (pp. 317–321); and for each gill a special cranial nerve or nerve branch (cf. Figs. 374, 375, pp. 383, 384). Stillening the gill and extending outward in sharks is a gill septum of connective tissue, which externally becomes a fold of skin overalpning and protecting the gill next posterior to it. The gill itself is a richly vascularized structure covered by a thin epithelium, folded into numerous parallel gill lamellae.

A gill may develop on either side of any gill slit or, stated in another fashion, may develop on either surface of a gill arch (Fig. 229, 4). In most cases an arch carries a gill on both surfaces, and is hence considered to be a "complete" gill, a holobranch. Less commonly in fishes, a gill may be developed on only one surface of a gill arch, which is hence termed a hemibranch. No vascular arch is commonly present behind the last gill slit and in consequence there is almost never any gill development on the posterior surface of the last slit. All other typical slits in sharks, however, bear gills on both sides; in terms of gills (errurens of gills (errurens of gills) errurens of gills on the sides in the terms of gills or the sides of t



Fig. 228. Horizontal sections through the head and pharyax regions in embryos of A, a frog (Rana); and B, an elasmobranch; to show development of gill pouches. In A the pouches are developing as anzerow silts, which have not as yet opened to the surface. (The month is also closed). In B all the silts except the last one are open, A, Espohagus; e.g., external gill developing, A, hyoid arch; M, mouth; m, man-diblast arch; A, A, pharyax; a, spincular gill sit; I to S, postspirecular slits.

than slits) there are thus four holobranchs. There is no gill development on the posterior side of the spiracle; hence the hyoid arch behind it is a hemibranch.

The spiracle is a small gill opening lying between mandibular and hyoid arches, Presumably this was a fully developed slit in ancestral types, but in all living jawed vertebrates the hyomandibular, as we have seen, comes to be connected with the jaw joint, and any opening between mandibular and hyoid arches in consequence restricted in development. Even in its reduced state the shark spiracle bears a small gill on its anterior margin. However, the blood which reaches it comes from the next gill behind it, where it has already been aerated, and the spiracular gill is thus thought of as a "false" gill, a pseudobranch. In the skates and rays the spiracle is enlarged and serves a useful purpose. These forms are bottom dwellers, in which the mouth is for much of the time buried in mud or sand; the spiracle is put to use as a substitute place of entrance for the water current.

The gill slits of clasmobranchs arise embryologically in a fashion characteristic of vertebrate generally (Fig. 228, B). Early in development paired pouches push out from the endodermal lining of the pharyngeal region and come in contact with infoldings of the surface ectoderm. Presently the intervening membranes break down, and the two epithelial layers join to form a continuous lining for the gill slits and, later, the folded gill membrane. In most cases the ectodermal part of the lining is responsible for the formation of the gill structures. The gill pouches form in paired longitudinal series and are basically responsible for a segmental arrangement of the associated nerves and skeletal structures. Many workers have attempted to correlate the gill segmentation with that seen in the myotomes and the skeletal and nervous elements associated with them. There is, however, no

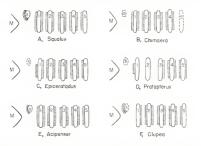


Fig. 229. Diagrams to show the gill arrangement. A, Shark; B, a chimace; C, the Anstralan lungfish; D, the African lungfish; E, sturgeox; F, a teleout (herring). Broken line indicates a closed skit. Hatched area adjoining slit indicates gill surface; verical line through hatching indicates pseudobranch. The presence in Protopterus of a gill surface on the posterior side of the last skit is unique. M, mouth: s, spiracle; postpericated skit sumuleror.

conclusive evidence of any real relation between the two systems of segmentation (cf. Fig. 179, p. 204).

The gill slits of elasmobranchs open directly and independently to the surface, but in the related chimaeras there develops a fold of skin, an operculum, which, extending backward from a point behind the jaws, covers and protects be gill series. We may note that chimaeras (Figs. 22, C, p. 42; 24, p. 44; 229, B) differ from their shark cousins in two further respects—the spiracle has disappeared (as it has in a few sharks as well), and the last gill slit is closed.

Gills in Jaceless Fishes; Gill Origins. Descending the evolutionary scale from the sharks, we find that in lampreys and hagfishes (Figs. 226, A, B, p. 244; 231) gills are equally well developed, but in a rather different fashion.

Fig. 230. Two lamellae from the gill of an eel; the large cells at the base of the lamella are salt-secreting. (After Keys and Willmer.)

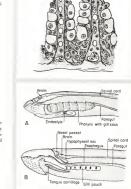


Fig. 231. Sagittal sections of A, the ammocoete larva of a lamprey; B, adult lamprey; to show especially the division of the adult pharynx into two parts. The endostyle of the larva becomes the thyroid gland of the adult (not shown). (After Goodrich)

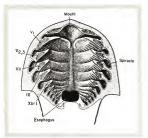


Fig. 232. Restored view of the pharpsenging of a late Silurian ottenederm of the cephulaspid type; the "head" viewed from below after he removal of the bones of the "furst" (cf. Fig. 19,  $B_c$  p. 38). The month is tiny, the pharps an expanded foodstraining device,  $V_c$ ,  $V_c$ ,  $V_c$ ,  $V_d$ , V

The gill passages are not slits but spherical pouches, connected by marrow openings with the pharynx, on the one hand, and the exterior on the other; and the gill lamellae, in the adult, form a continuous ring around each pouch. There is a well-developed musculature which effects a pumping movement on the sacs, so that water can be drawn in through the external tubes and forced out again through them, allowing the gills to function even when the animals mouth is occupied with its prey. Further devices to aid simultaneous feeding and breathing are present in both lampreys and hagishes. In the adult lamprey the pharynx splits into two tubes; a small dorsal duct leads directly back from mouth to esophagus, by-passing the gills; these lie in a larger, ventral pharyngcal sac which ends blindly at its posterior end. In hagishes an equally peculiar device is present. The combined nostril and hypophyseal pouch breaks through posteriorly into the roof of the pharynx.

In most cyclostomes we find a higher number of gill pouches than the normal ganthostome count of five slits plus a spiracle. Petromyzon has seven pairs of pouches; hagshes from six to fourteen. There is variation in external openings as well. In lampreys and the slime hag Bdellostoma each gill pouch opens by a separate orifice; in the common hag, Myxine, in contrast, the whole series of tubes of either side fuse externally to form a single outer opening.

The Ammococtes larva of the marine lamprey, we have noted, spends its existence half buried in the mud of streams and ponds; it feeds on minute food particles which are collected from the water passing through the pharynx and gills in a fashion similar to that seen in Amphioxus and the tunicates. It is apparent that here this food-collecting function of the gill system is a more important one than that of respiration, which could be readily carried on in the skin of these small animals. This situation, reinforced by the facts discussed in Chapter 2, leads to the concept that food collecting was the primary raison d'etre of the gill system and respiration was a first only an accessory function.

Further evidence that food gathering was a major function of the gill system not only in their lower chordate ancestors but in ancestral true vertebrates as well can be adduced from a study of the most ancient of vertebrates, the fossil ostracoderms (Figs. 18, 19, p. 38). In such forms as the cephalaspids (Fig. 232) the mouth was small and apparently without means of aggressively gathering food, but the gill pouches (here about ten in number) occupied an enormous chamber on the under surface of the "head" region, and were obviously far larger than need have been the case were they concerned with respiration alone. It is obvious that these early vertebrates were still filter feeders, and that it was not until jaws (or the evolostome substitute for them) evolved that this mode of alimentation was abandoned and the gills assumed their role of purely respiratory organs.

Pharynx and Gills in Bony Fishes and Tetrapods. In the bony fishes the gills (Fig. 226, D. p. 244) are basically similar to those of sharks; but there are various differences, due in part to the fact that in all members of this class of fishes there is a highly developed operculum, here (in contrast to chimaeras) reinforced by bony plates (Figs. 106, p. 141; 134, p. 181; 157, p. 183). Beneath the operculum there is present a considerable branchial chamber. In sharks, breathing is accomplished by (I) expansion of the pharynx with gill slits closed and the mouth open, with the effect of drawing in a volume of water, and, (2) constriction of the pharynx with the mouth closed, thus forcing the water out the open slits, past the gills. In most bony fishes the action is similar, except that it is the opercular opening that is closed and opened rather than individual slits. Since the gill region is protected by the operculum, the flaplike development of the gill septa present in sharks is reduced (Fig. 227, B. p. 245s).

Normally teleosts have five pairs of typical gill slits as do sharks, but aberrant conditions are occasionally found. There tends to be some reduction in the number of gills present (Fig. 229, C-F). In teleosts, for example, no gill is developed on the anterior margin of the first slit, and gills are much reduced in African and South American lungfishes. That the spiracle was present in primitive bony fishes is attested by its presence in the most primitive ray-finned forms —Polypterus, sturgeons and paddlefishes. The spiracular opening is lost, however, in all other living Osteichthyes, although (curiousty) a small gill may persist in the teleost pharvax near the site of this lost opening.

The gills of teleosts have excretory as well as respiratory functions. Glandular cells of the gill membranes (Fig. 230) appear to excrete nitrogenous wastes, supplementing the work of the kidneys. An important function of such cells in marine teleosts is their ability to excrete salt, further aiding the kidneys in maintaining a proper "internal environment" in which too high salt concentrations are harmful (ef. pp. 278–279).

In the larvae of a few fishes—Polypterus and the African and South American lungfishes—and in most amphibians as well, there are present accessory respiratory organs in the form of external gills. As seen in the fishes mentioned [Fig. 233] and in urodele amphibians, they are feathery processes, from one to four in number, which grow out of the side of the "neck" region above the gills; in life they have a reddish color, due to the presence of an abundant blood supply. The citation of the specific fishes which have these organs is in itself sufficient to bring to mind the most probable reason for their existence—that they are structures which add in obtaining the utmost in oxygen from waters stagnant because of drought. (It is, of course, during the rapid growth characteristic of embryonic and larval periods that oxygen demands are at their height.) It appears probable that these larval structures were characteristic, as were lungs, of the ancestral bony fishes, only to be abandoned later by most members of the group.



Fig. 233. Larval form of the primitive African ray-funned fish, Polypterus; the large external gill extends back above the pectoral fin. (From Dean.)

In the Amphibia they are present in typical fashion in urodeles and the Apoda as well. In anurans external gills begin to develop at an early stage, but later the gill region of the two sides is enveloped by a great fold of tissue, termed an operculum but not homologous with that structure in a fish. Beneath it there is a mass of filamentous gill tissue which appears to be derived in part from external gills, in part from outgrowths of the internal gill structures.

With the appearance of lungs, followed by the evolution of life on land, we find in adult amphibians and in all ammiotes a great reduction in size and importance of the pharyax. In amphibians gill slits break through to a variable degree in the larvae, but internal gills never function (except in hir aberarant condition we have noted in frogs), and apart from persistently larval forms the slits disappear in the adult. In ammiotes, gill pouches are always formed in the embryo and push outward, as in fishes, to meet surface furrows of ectoderm; but gill slits open only in a transitory manner if they open at all. The ammiote embryo, in conservative fashion, repeats the embryologic processes of countless ancestral generations; but never is there any true outogenetic repetition of the development of the full-blown adult gill system found in the fish ancestor.

In the adult amniote, as was said in the introduction to this section, the pharynx retains hardly a vestige of its former importance. The lungs developed from the pharynx in fishes, and the lung entrance is still to be found in the pharyngeal floor. Of the gill pouches, the spiracle persists in modified form in connection with the ear, in the adult amniote the other pouches have disappeared completely.

### THE SWIM BLADDER

Characteristic of most ray-finned fishes is the presence of a swim bladder, an elongate sac arising as a dorsal outgrowth from the anterior part of the diges-



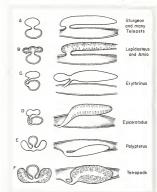
Fig. 234. Diagrammatic longitudinal sections of the air bladder in various teleosts. A, Primitive type, open to the gut; B, C, closed types, with gas-producing red body and other areas for gas resorption.

tive tube; this is usually distensible and is filled with air or other gases (Figs. 234, 235, 4-6.). Its major function is that of a hydrostatic organ, filling or emptying this sac alters the specific gravity of a fish and aids it in keeping at a depth in the water proper to its habits. It is thus obvious that this structure is most useful to fishes living in deep-water bodies—most especially the ocean. Polypterus, most primitive of actinopterygians, has no swim bladder as such but has, instead, ventral paired lungs; all other actinopterygians, however, have this air sac, except where it appears to have been secondarily lost in some teleosts. It seems certain that the swim bladder is a specialization of the ray-finned fishes, developed at an early stage in their history; it is found in no other fish group whatsoever.

In its most primitive condition the air bladder connects with the pharyux by a pneumatic duct through which, when the fish rises to the surface, air can be taken into the sac, and through which the air can, as well, be discharged. In more specialized teleosts, however, this tube may be shifted to a more posterior connection with the digestive tract. In many advanced teleosts such connection has entirely disappeared; in such forms the walls of the swim bladder become specialized as a retort which can fill the bladder with gas, and a specific area is also present in which the gas so formed can be resorbed (Fig. 234, B-C).

In some cases—notably the relatively primitive actinopterygians Amia and the gar pike—the air bladder is rather lunglike in texture (Fig. 235, B) and is an auxiliary breathing mechanism. This suggests the possibility that air breathing may have been the original bladder function. In its dorsal position and single

Fig. 235. Diagrammatic cross sections and longitudinal sections of the air bladder or lung in various fishes and in tetrapods. A, Typical dorsal air bladder of actinopterygians; B, a bladder type found in holosteans with a folded inner surface capable of some breathing function; C, an unusual teleost type with a lateral opening suggestive of a transition from lung to air bladder; D, the Australian lungfish, with the bilobed lung rotated dorsally, although the opening remains ventral in position; E, the archaic actinopterygian, Polypterus, with a ventral lung, probably primitive and antecedent to all other lung or air bladder types; F, the type of lung developed in land vertebrates, with complex internal structure. (After Dean.)



rather than paired nature the swim bladder contrasts strongly with the lungs. However, most anatomists believe that the two are in some fashion and to some degree homologous structures. We shall discuss this further after a consideration of the history of the lungs.

### LUNGS

Lung Structure. Structurally distinct from the gills, although similar in basic function, and, like them, pharyngeal derivatives, are the lungs, which in typical air-breathing vertebrates replace the gills as the medium through which oxygen is brought to the blood and tissues. In most tetrapods the air-breathing apparatus has a characteristic pattern which may be sketched at this point (Fig. 236). Entrance to the air duct is gained by a median ventral opening in the pharynx, the glottis. Immediately beyond the glottis the duct enlarges to a chamber termed the larynx; beyond this a ventral median tube, the trachea, extends backward to divide into primary bronchi, one leading to each lung. The paired lungs, primitively ventral, may expand to occupy a lateral or even dorsal position in the anterior part of the celomic cavities. Embryologically the lung structures appear as a median ventral outpocketing of the floor of the throat at the posterior end of the pharynx. This is in many cases distinctly bilobed at an early stage; the lung buds grow backward, accompanied by connective tissues which strengthen their walls and may produce skeletal elements related to larvnx, trachea and bronchi.

In addition to an internal epithelium of endodermal origin, the lungs include in their substance variable amounts of connective tissue and smooth muscle fibers and, of course, an abundance of blood vessels of the special pulmonary system; externally they are covered by epithelium of the body cavities within which they lie. The efficiency of a lung depends in the main upon the amount of internal membrane surface present for gas exchange. Birds and mammals, with greater activity and greater needs for oxygen, increase the exchange area not so much by

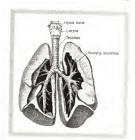


Fig. 236. Ventral view of the respiratory system of man. The lungs dissected to show the bronchi, (After Toldt.)

increasing lung size as by increasing the complexity of internal subdivision. Here, as usual, we must keep in mind the problem of surface-volume relationships; in large animals the lungs must be disproportionately increased in size or attain greater complexity of subdivision so that the exchange surface may keep pace with the volumetric growth of tissue demanding oxygen.

It may be noted, parenthetically, that lungs are not the only possible media for obtaining atmospheric oxygen; any thin moist membrane may effect gas exchange. In the modern amphibian orders the skin, as has been mentioned, is an important breathing structure and is richly supplied with blood vessels; in frogs and toads much of the breathing takes place through the moist membranes of the mouth. Even a variety of teleost fishes, such as the "tree climbing perch" (Ana-bas) of the East Indies, is able to breathe air by structures developed in or from gill chambers, kept moist beneath the oper-culum.

Lungs in Fishes. Although lungs are most characteristically developed in tetrapods, they are phylogenetically older structures. Lungs are present in the dipnoans, who gain their popular name of lungishes from this fact, and surely were present in their close relatives, the ancient crossopterygians, from which land animals are descended. Still further, lungs are present in Polypterus, the most primitive of all members of the ray-finned group of bony fishes.

Fish lungs (Figs. 235, D. E. p. 251; 237, A. B) are simple in construction. In Polypterus an opening in the pharyax floor leads to a bliobed sace the lobes as back on either side of the esophagus. Except for the elongation of one lobe they resemble the lungs of amphibians and appear to be quite primitive in nature. In dipnoans there is some modification, for although the opening, as always, lies in the floor of the pharynx, the duct curves upward around the right side of the pharynx, so that the lungs, (which may be partially or entirely fused to form a single until are dorsal in position. The course of the duct suggests that the dorsal lung position is a secondary one. This supposition is reinforced by considera-

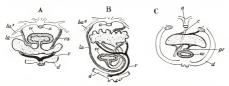


Fig. 237. Diagrammatic cross sections of bony fishes (seem from behind) to show the position of the lung or wrism bladder and the blood vessles connected with it. A Polypterus, a primitive actinioperygian, with a ventral paired lung. B. Epiceratodas, a lungfish, with a single lung dorsal in position, but with a ventral paired lung. B. Epiceratodas, a lungfish, with a single lung dorsal in position, but with a ventral opening from the gut C. a teleout with air bladder (due loss), the blaug, the sarial supply is from the last aordic arch; in B the curve of the vessel from the left arch below the gut in cates the path of dorsal migration of the lung. In the teleout the arterial supply to the air bladder is from the dorsal aorta (by way of the celias artery.). In the lung the venous return is directly to the heart region. The Epicentosia veries show an asymmetrical condition comparable to that of the arteries. From the air bladder the blood returns to the heart via the normal venous system. a, Dorsal sortic arch; c, cello artery, whose the ranches run to teleoat air bladder; d., common cardinal vein (duct of Cavier; lie. left pulmonary artery; c, ecoplague; pr, portal vein, draining part of teleoat air bladder; d., right pulmonary artery; c, and construction of the co

tion of the blood supply; part of the lung is supplied by an artery (Fig. 237, B, la) which follows the presumed phylogentic migration path in looping ventrally around the esophagus from the left side of the body to reach the lung.

The embryonic development of lungs suggests that they arose in phylogeny as pockets of the moist pharyngeal epithelium which became specialized for absorption of atmospheric oxygen. But when and why did they arise? Since they are found in both the Sarcopterygii and the most primitive of actinopterygians, they obviously date in time from a very early stage in fish history; there is even evidence suggesting their presence in the very ancient placoderms—a group at the very bottom of the scale of jawed vertebrates. Presumably the conditions of seasonal drought which we have previously noted to have been dominant in the early days of fish evolution may have been responsible for their evolution as accessory breathing organs when waters became stagnant or streams dried.

If, as we assume, lungs and swim bladder are homologous, which is the ancestral type? Early writers took it for granted that since the swim bladder is a fish structure and lungs primarily characteristic of tetrapods, the swim bladder was the progenitor of the lungs. But consideration of the evidence now available points to the probability that the reverse is the case: the lung is primitive, the swim bladder a derivative evolved during the evolution of the ray-finned division of the bony fishes, in which group alone it is to be found. This is readily correlated with known facts in their history. The lung has been retained as such in modern fishes only in a few forms still living in tropical regions of seasonal drought. Most actinopterygians do not live, either in fresh waters or occan, in regions where such conditions now maintain. A lung is of little or no use to such fishes; but if converted to a dorsal bladder, it could—and has—become a hydrostatic organ, especially useful in the marine environment in which most later actinopterygian evolution occurred.

The Lungs in Tetrapods. In amphibians the lungs remain relatively simple structures, with little internal subdivision (Fig. 238, A). Many reptiles show little further advance (Fig. 238, B), but in some lizards and in turtles and crocodilians there is multiplication of septa and internal partitions to give a more complex structure and a rather sponge-like texture. In modern amphibians, in default of ribs, the lungs are filled by "swallowing" air—a force pump mechanism. In most reptiles the ribs are raised by trunk muscles, the abdominal cavity in which the lungs lie is expanded and air is thus brought in by suction (Turtles, encased in a solid shell, rely mainly on special abdominal muscles for lung action.)

In birds the lungs themselves are small and compact but the breathing ap-

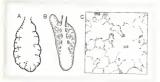


Fig. 238. Diagrammatic sections through the lung of A. a frog, and B. a lizard. C. Section of a small area of a human lung. xabout 50, showing its complex construction. ad. An alveolar duct, smallest component of the duct system, a. one of the alveoli to which it leads. (A after Vialleton; B after Goodrich.)

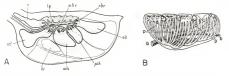


Fig. 29. 4. Diagram of the trusk of a bird, left side view, to show the position of the respiratory gases a.9. Absonned air was eth. intend air was eth. intend air was eth. intend air was eth. gas the star i.e. it intends are set. g., left lung; nhe, bronchus running through the lung and leading from traches to various air sets ph. posterior thoracic air set, for, recurrent bronchis which return air from sec to respiratory are sets ph. posterior thoracic air set, for, recurrent bronch which return air from sec to receptating areas of lung. B., Lateral view of the left lung of a bird. The primary broachus, h traceres the length areas of lung. B. attent lives of the lung to the absonned as a Bronches are given of leading to other air seas and not paraches are given of leading to other air seas and not paraches. I we procession. Left deep consiste B after level was Intends.

paratus is complex in structure and function. Out beyond the lungs there develop, some four pairs of air sacs which invade every major part of the body (Figs. 239, A, 240), and even beyond these sacs there may be air passages invading elements of the skeleton. The sacs themselves absorb little oxygen but nevertheless play a major role in respiration. Air is drawn in by raising the ribs and consequently expanding the trunk volume; it passes inward through the lungs, by channels continuous with the bronchi, to the air sacs. Respiration mainly takes place on the "return trip" from the sacs; small channels lead from the air sacs to the lung respiratory passages and surfaces and thence outward to the bronchi. The internal structure of the bird lung is likewise unique (Fig. 239, B). In other anniotes the respiratory membranes are in "dead-end" alveoli. Nothing of this sort is found in the bird lung every passage, large or small, is open at both ends, so that there is a true circulation of air.

In mammals the lungs are large, occupying a considerable area in the thorax, but show a rather simpler pattern than that found in birds. They are finely subdivided into tiny and exceedingly numerous alreoil (Fig. 238, C) to which the air passes by means of a branching series of larger and smaller bronchi and, finally, bronchioles; the alveoli cluster about the terminal ducts like grapes on the stem. In the embryo mammals (Fig. 241) the primary lung bud invades a

Fig. 240. Ventral view of the lungs of a bird to show the connections with the various air sacs



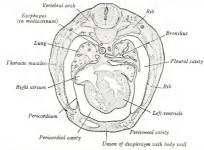


Fig. 241. Cross section of a human embryo (at eight weeks) to show the development of the lungs and of pleural and pericardial cavities and heart. (From Arev.)

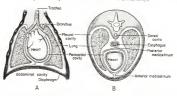


Fig. 242. Diagrammatic longitudinal, A, and cross sections, B, of the thorax in mammals to show the position of heart and lungs and of pleural and pericardial cavities.

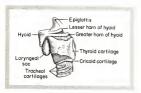
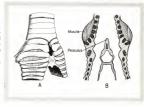


Fig. 243. The laryux of the rhesus monker, in side view. The broid apparatus, with its greater and leaser horas, is seated above and anterior to the laryux. The rhesus monker has a resonating chamber in the laryugeal sec. Shown are the thyroid and cricoid cartilages, trached cartilages, and a membrane connecting the hyoid and the thyroid cartilages. A muscle runs from thyroid to-critical and covers most of the latter, there are several other small muscles proper to the laryux more deeply situated and not shown. (After Hartman and Straus: Anatomy of the Rhesus Monkey, Williams and Wilkins Co.)

Fig. 244. The syrinx of a songbird (magpie).

A. External view; B, in section. Vibratory membranes on the inner aspect of the two bronchis meet at the base of the trachea to form the median pessalus; further membranes may develop between the expanded rings at the tracheal forks. The syrinx is controlled by musculature of the hypotranchial group. (After Hacker.)



compact mass of mesenchyme, within which, by repeated budding and subdivision of cavities, the adult structure is eventually attained. Breathing is accomplished by a highly efficient suction mechanism (paralleled to some degree by crocodilians and birds). The lungs no longer lie in the general abdominal cavity as they do in primitive tetrapods; instead each lies within an individual pleural cavity, closed off posteriorly by the development of the diaphragm (Fig. 242; ed. p. 228). Expansion of the cavities, and consequently of the lungs, is attained as much or more by downward movement of the diaphragm as by movement of the rib basket.

With the rise in importance of the lungs in land vertebrates, the larynx (Figs. 209, p. 232; 243), surrounded by a complex of cartilages or bone, arose as its vestibule; and a flap of skin, the epiglottis developed to cover its entrance in mammals. Frogs and toads, a few lizards and, notably, most mammals have acquired a voice through the development of elastic ridges, the vocal cords, stretched across the larynx. In birds no such cords develop, but voice production occurs in an organ, the syriax (Fig. 244), typically developed farther down the throat at the point of subdivision of the trachea. With the development of the neck in tetrapods the originally short duct from throat to lungs becomes the elonate trachea, its walls generally stiffened by cartilages which in amniotes are ring-like structures. In amniotes the trachea divides into two primary bronchi before the lungs are reached.

### PHARYNGEAL DERIVATIVES

The pharyax is important in every group of vertebrates as the embryonic source of glandular structures. For the most part they are derived from the epithelial walls of the gill pouches (Figs. 245, 246), and form varied masses of tissues present in the throat region of the adult. Most of these glands are endocrine in nature; their description is deferred to Chapter 17.

Thymus Gland. There is no formed thymus in hagfishes and its presence in lampreys is doubtful; otherwise it is universally present, often prominent, and seemingly important but of uncertain function. It consists of clusters of soft glandlike tissue found in variable arrangement in the gill or throat region. When well developed, the thymus is formed into lobules, each containing a cortex that is filled with lymphocytes and a medulla in which a reticular tissue is prominent

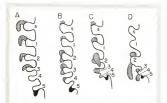


Fig. 24.5. Diagrams of the gill pouches of the left side of the pharyns in d. a shark, B. a wrodeler, G. a lizard, B. typical manuals; to show the derivation of thymus, parathyroid, and ultimobranchial lodies. The dorsal part of each grill pouch is, for purposes of the diagram, all the upper side. Broken outline, visited hatching, order to the proper side of the properties of the provide of the properties of the properties of the provide side black, ultimother solid, ultimother solid, s. Spiracular pouch. (Mainly after Maurer.)

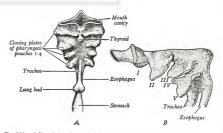


Fig. 246. A. Ventral view of a model of the anterior part of the gat tube and its outgrowths in an embryo anamal (Homo). B. Lateral view of the pharva: in a slightly later embryo. Closing plates separating tips of gill pouches from the surface are hatched; pouches, including the spiracular pouch (mid-dle ear), indicated by Roman numerals. (From Arex.)

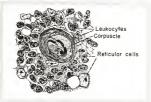


Fig. 247. A small part of a mammalian thymus, showing the numerous white blood corpuscles, the cells forming the reticulum and one of the peculiar corpuscles characteristic of the gland. (After Dablgera and Kepner.)

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(Fig. 247). In fishes, thymus material is generally present, deep to the surface, above most or all of the gill slits. In most tetrapods thymus tissue, in varied shapes—other as two pairs of tissue masses—is present in the neck; in mammals it generally consists of a single pair of glands at the anterior end of the horax, deep to the sternum. The thymus is, in part at least, derived from thickenings of the epithelium of the embryonic gill pouches, generally from their dorsal margins. There is, however, much variation as to the pouches involved; in fishes every typical gill pouch may produce thymus material, but in tetrapods only one or two pouches are involved. In mammals the second postspiracular gill pocket is the usual seat of thymus origin, and here it buds from the ventral rather than the dorsal margin of the pouch. The reticular tissue of the gland seems definitely to originate from the epithelium, but the lymphoid cells develop (as do other blood cells) from mesenchyme.

The gland grows rapidly during embryonic life, but before the adult stage is reached, the thymus ceases to grow, in tetrapods it may undergo degeneration and in many adult mammals the thymus has disappeared entirely. Despite much work we know little of thymus functions, other than the fact that it seems to be a seat of origin of white blood cells, at least in the young.

## 12

### DIGESTIVE SYSTEM

The mouth and pharynx, described in the last chapter, are the forward outposts of the digestive tube, with gathering of food materials as their original major duty. The business of digestion is the function of the remainder of the digestive tract, to which the ancient and simple Anglo-Saxon term "gut" may be properly applied. The gut, so limited, together with its outgrowths—liver and pancreas—will be considered in the present chapter.

Gut Functions. The functions of the gut may be considered under four heads: (1) Transportation. Once food materials are gathered, they must be carried along the "dis-assembly line" of the successive gut sectors, and wastes must be ultimately disposed of as feces. Although cilia are present in the gut epithelium in some instances, transportation is mainly the function of the visceral musculature which surrounds the digestive tube for its whole length-mostly smooth muscle, but often to some degree striated at the anterior end of the gut. The smooth musculature, usually arranged in sheets of both longitudinally and circularly arranged fibers, is influenced by nerves of the autonomic (involuntary) system but in great measure operates independently of central nervous control. The major muscular activity causing movement of food materials is peristalsis-successive waves of muscular contraction causing constrictions of the gut which travel backward and push the food before them. (2) Physical treatment. Food may enter the digestive tract in large masses which must be reduced in size before an efficient chemical attack on them can be made; effective here (in contrast to peristalsis) are rhythmic contractions of the gut musculature. This "squeezing" of the food masses, together with the addition of mucus from the gut walls, reduces the food to a soft pulp, chyme. (3) Chemical treatment. This is digestion in the technical sense, the breakdown of potentially useful "raw materials" in the food to relatively simple substances which can be utilized by body cells. Water and necessary salts are readily absorbed by the intestinal lining; other needed materials-simple sugars, fats, amino acids-generally enter the gut in the form of complex compounds which must be broken down into simpler units before they can be utilized by the cells or even absorbed through the gut walls into the circulatory vessels. This breakdown is produced by enzymes, secreted by the cells

of the gut and its outgrowths but mainly doing their work by being released into the gut cavity and attacking the food materials there. (4) Absorption. When this chemical breakdown is accomplished, the products are absorbed by the intestinal wall for circulation to body cells and storage areas; sugars and amino acids pass via veins to the liver and thence to the heart and body, while part of the fats reach the general circulation by way of lymphatic vessels.

Development. In Chapter 5 was described the formation, in one fashion or another, of an archenteron, or primitive gut. In Amphicous (Figs. 52, p. 89, 66, p. 101) this is from the first a simple cylindric pouch; in mesolecithal egg types, such as amphibilians, the early gut is similarly constructed except that the gut floor is distended in paunchy fashion by a mass of gut cells rich in yolk (Fig. 70, p. 106). In telotecithal eggs, however, the presence of a great amount of yolk causes a radical change in early gut development. In early stages the gut lining does not form a closed tube but is spread out over the yolk, which it eventually encloses in a sac which is an extension of the gut cavity; only later does the entrance to the sac become constricted and the gut assume a tubular shape of yolk, follow this same pattern of development and produce a yolk sac, although an empty one; and in all ammiotes there is a second, more posterior diverticulum from the gut, the allantois, from which in the adult arises the urinary bladder (Figs. 63, B, D, 74, p. 108, 248, 249).

In all cases, however, the gut eventually becomes a tubular structure. In most forms it remains for some time closed at both ends. As noted in the last chapter the anterior end eventually breaks through to connect with the mouth depression. Posteriorly, many vertebrate types, we have seen, have in the gastrula stage a posterior opening, the blastopore, which is in approximately the region of

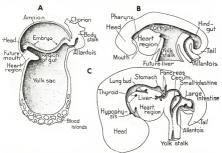


Fig. 248. Diagrams to show the development of the digestive tract in a mammal (Homo). A, Stage somewhat later than that of Figure 63, C; B, stage slightly later than that of Figure 63, D; C, an embryo of about the age of that in Figure 74. (After Arey.)

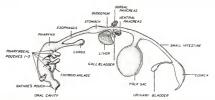


Fig. 249. A diagram of the digestive tract and its outgrowths in an amniote embryo similar to that of Figure 248, C, but with the structures concerned shown as solid objects rather than in section. (After Turner.)

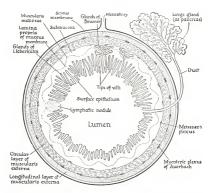


Fig. 250. A diagram of a generalized cross section of the gat. In the upper half of the drawing the murcous membrane is provided with glands and villi; in the lower half it contains only villi. Meissner, is plexus (submurcous plexus) and the myenteric plexus are part of the autonomic nervous system, to take the more of the plant of the more area of the more and the section of the section of the villing of the submurcous testeds outward as far as the muscularis nucesac; it is followed outward in the section by the submurcous tissue, the nuscular tancie, in two layers, and finally, the secrets tanic. The glands of Brunner and of Lieberkihn are two types of glands characteristic of the mammalian small intestine. (From Maximos and Bloom.)

the anus or cloacal opening of the adult, but in large-yolked types this opening is at best transitory in nature. In any case the blastopore soon closes, so that the gut ends blindly, posteriorly as anteriorly, for much of embryonic life. Analogous to the development of the stomodeum anteriorly is the appearance posteriorly of the proteduem (Fig. 206, p. 230), an indipping pit of ecodorer beneath the tail; this is separated from the distal end of the gut tube by a membrane which eventually disappears. Meanwhile, within the gut there occurs a lengthening of the tube and a differentiation of successive regions into adult organs (Figs. 248, 249). Of these regions he most anterior, the pharynx, has been described previously and the most posterior division, the closea, is so intimately associated with the urinary and genital as well as digestive systems that its consideration is best postponed. Subtracting these regions, there emain for consideration the major segments of the endodermal tube to which the term gut is for present purposes restricted.

Gut Regions and Tube Structure. A study of higher vertebrates gives one the impression that the succession of structures along the gut is consistent and uniform: esophagus, stomach, small intestine, large intestine, and on to rectum and arus. But when we extend our view to lower groups the picture becomes confused (Fig. 251). The distinction between large and small intestine breaks down in primitive vertebrates; the esophagus may be vestigial or absent; in some fashes there is no stomach. In Amphioxus and cyclostomes the postpharyngeal gut is essentially a single tubular unit; most familiar landmarks are absent.

It is, however, possible at least to distinguish two successive regions of this tube in all vertebrates. Between stomach and intestine there is generally found a distinct pyloma, a constriction, usually muscular, which guards the gateway into the intestine. In instances where this is poorly developed, the fact that the bile duct from the liver enters just back of the pylorus enables us, even so, to establish a line of demarcation. We shall here term the region anterior to the pylorus the foregut and the intestinal area beyond, the hindgut, frimitively, it would seem, the hindgut, forming the intestine, was alone concerned with digestion and absorption of food, and the foregut was little developed. In advanced vertebrates we see an increasing growth of importance of the foregut, with, first, the development of the stomach in most vertebrates and, secondly, clongation of the esophagus in tetrapods.

Although highly variable from region to region and from form to form, certain general characteristics may be found in most regions in the detailed structure of the gut tube (Fig. 250). The inner surface is a macous tunic; this consists mainly of the gut epithelium, only one cell in thickness in many regions and generally mucus-producing in part; this epithelium further forms varied glands extending out from the gut tube. Beyond this is the submucous tissue, misnify formed by connective tissue, with numerous included blood vessels. A muscular tunic generally includes two layers of smooth muscle, the inner a circular layer and the outer a longitudinal one. Most of the gut lies in the abdominal cavity of the celom, and hence is surrounded externally by a serous tunic of celomic epithelium backed by connective tissue.

Esophagus. Not only in Amphioxus and cyclostomes, but in a fair numher of jawed fishes as well—chimarca, lungfishes, certain teleoust—the entire foregut is simply a tube interjected between pharynx and intestine. Although both esophagus and stomach develop from this tube in more progressive vertebrates, the term "esophagus" may, in default of stomach development be applied here to

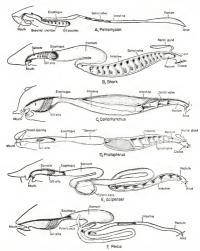


Fig. 25.1. Digestive tracts of A, a lamprey; B, a shark; C, a chimaera; D, a lungfish; E, a sturgeon: F, a teleost (perch). The "stomach" of the lungfish is nonglandular and is simply a somewhat enlarged section of the ecophagus. (From Dean.)

the whole of the simple foregut. In all other living fishes—elasmobranchs and most rayfuned forms—the development of a stomach leaves only a short and ill-defined length of tube anterior to it to be considered as an esophagus. In land vertebrates, however, reduction in length of the pharynx (with loss of gill breathing) and the concomitant development of a neck, frequently of some length, bring into being a well-defined tubular esophageal gut segment. Only exceptionally has the esophagus any function other than that of transportation of food. Except for mucous cells, glands are little developed; the epithelium is generally of a tough stratified type, but in some cases cilia are present, even in the adult. There is a stout muscular coat which is generally composed of smooth musculature, but in many fishes and again in mammals there is striated musculature, although this is of visceral origin (cf. p. 216). Two unusual developments may be noted. In

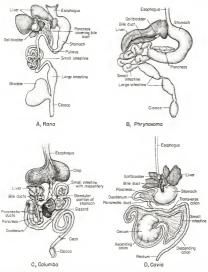


Fig. 252. Diagrams of digestive tract and appendages, seen in ventral view in A, a frog; B, a reptile; C. a bird (pigeon); D, a mammal (guinea pig). (A after Gaupp, B after Potter; C after Schimkewitsch.)

lampreys the pharyux, we have seen, splits into two parts, the lower becoming a blind pocket for the gills, the upper giving a long anterior extension to the esophageal tube (Figs. 231, B, p. 247; 251). In birds a distensible sac, the crop (Fig. 252, C), develops part way down the esophagus. It serves as a place for temporary storage of grain and other food and in doves exudes a milky material with which the young are fed.

Stomach. Although we are accustomed to think of the stomach as a normal part of the gut, it is absent in various lower forms, not only Amphioxus but a number of fish types—cyclostomes, chimaeras, lungfishes, and some teleosts.



Fig. 25.3. Diagrams to show stomach form and nature of internal lining in A. a shark; B. a teleost (seel); C. a submarder, B. a turble, S. a hard (percock-the thickword wall of the giverand is indicated); F. man; G. a have; H. a ground squirrel; I. the concy of Africa; J. a whale; K. a kangaron; L. ac. L Epithelium of coolspaced type (cilitated in C) which may poenter into stomach, particularly in mammals; 2, cardiac epithelium (found only in some mammals); 3, fasthe epithelium, 4, pubric epithelium. (Afree Pernhopel)

When present, as in all other vertebrates, it serves three functions: storage of food awaiting entrance into the intestine, physical treatment of this food, and initial chemical treatment of protein food materials. It is probable that in ancestral vertebrates, as today in fishes lacking a stomach, the last two of these functions were served by the intestine alone, and that the primary function of a stomach, when first developed in phylogeny, was for the storage of food masses which could not all be accommodated at once by the intestine. Such a situation would have first arisen when there developed, from early filter feeders, predaceous jawed forms, such as the sharks, which would bolt chunks of food in large quantities at triegular intervals. A pouch for food storage and physical treatment would thus become necessary; the introduction of digestive enzymes was presumably a phylogenetic "afterthought."

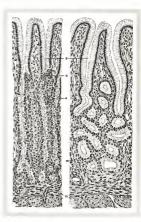
As regards external shape (Figs. 251–253), the central type of stomach structure, seen in various groups from shark to man, is one in which at the end of the esophagus the gut tube curves to the left, "descends," as a cardiac region of the stomach, to a major ssc, the fundus, and then "ascends" to the right as the pyloric region. It should be noted that the shape of a stomach in a dead, dissected animal may be quite different from that in life, and that marked changes may take place from moment to moment in an active stomach (Fig. 254).

Highly important is the nature of the epithelial lining of various stomach



Fig. 254. Skiagrams of a human stomach taken at intervals after food, showing its variable shape when active. (After Cole, from Fulton.)

Fig. 255. Left, a section of a portion of the fundes region of a mammalian tomach, showing the gastric pits (p) and the glands deep to the pits and operating into them Mucous cells the pits and operating into them Mucous cells glands, below, two cell types can be disagglands, below, two cell types can be disagguished: partical cells (a), secreting hydrochloric acid, and smaller and more lightly staining chief cells, producing pepsin, m, smooth muscle cells, for going pepsin, m, smooth m, smoot



regions (mucous cells are present throughout). An esophageal type of epithelium may be present in a proximal segment of the stomach which is presumably an area "borrowed" from the esophagus. In mammals alone there may be a transitional cardiac type of epithelium proximally which contains glands, but glands of little chemical importance. The fundar type of epithelium is characterized (Fig. 255) by the presence of numerous tubular glands which usually contain two types of cells—the so-called chief cells, producing pepsin, an enzyme aiding in protein breakdown, and the parietal cells, which furnish hydrochloric acid and give the pepsin a more favorably acid medium in which to work. The pylonic epithelium resembles that of the cardiac region.

268 THE VERTEBRATE BODY

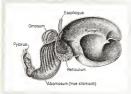


Fig. 256. The stomach of a sheep, sectioned to show the four compartments characteristic of higher ruminants. (After Pernkopf.)

There are numerous variations among vertebrates in stomach form and in distribution of epithelial linings (Fig. 253). The types of epithelial linings have no necessary relation to the similarly named morphologic regions of the stomach; for example, the stomach of man and mouse are much the same in shape but differ radically in the distribution of epithelia within them (Fig. 253, F, H). In most vertebrates the stomach is a relatively simple structure which may vary in shape from a straight, cigar-shaped tube, as in a variety of fishes and amphibians and the snakes, to a form, as in most teleosts, in which the fundus is a sharp V. Subdivisions of the stomach are found in some groups. In grain-eating birds there develops a distinct rough-walled muscular compartment, the gizzard (Figs. 252, C, 253, E), in which are contained small stones; this makes a grinding mill which functionally replaces the lost teeth. In the ruminating artiodactyl ungulates among mammals-such as cow, sheep, goat, deer and so forth-four distinct stomach compartments are present (Fig. 256). The first two, rumen and reticulum, are storage pouches where vegetable food is kneaded to a more workable pulp by action of muscular walls and subjected to the action of microorganisms, which break down complex plant materials and manufacture useful organic substances, some of which are absorbed in the rumen. At leisure the animal regurgitates the "cud" for chewing-or rumination, if you will-and then sends it, by a by-pass, to the omasum, where there is further physical reworking and, at long last, to a final compartment, the abomasum. Here alone (Fig. 253, L) are found the three types of epithelium proper to the mammalian stomach; it now becomes obvious that the three preceding compartments are not part of the original stomach, but essentially elaborations of the lower end of the esophagus.

the Intestine (Figs. 251, p. 264; 252, p. 265; 257, 258). The major stages in the true digestive process normally occur in the hindgui—the variably built intestine. More anterior segments of the digestive tract receive, transport, store and prepare food materials. In the intestine, however, occur most—and primitively, all—of the chemical processes of digestion. And here alone occurs, in most cases, the final crucial step, the absorption of food materials for body

In living vertebrates the intestine has come to share the production of digestive enzymes with other organs of the digestive tract. Many are formed in a special glandular outgrowth of the intestine, the pancreas; in most vertebrates the stomach has become a minor center of enzyme production, and even the salivary glands may take on such a function. Despite this, the intestine itself is still of

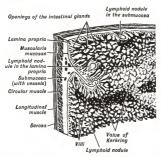


Fig. 257. Part of the wall of the mammalian small intestine. (After Maximow and Bloom.)

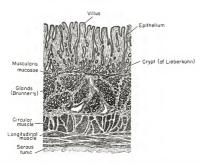


Fig. 258. A section through the lining of the mammalian duodenum, showing intestinal villi, the crypts between them, a thin muscle layer (the muscularis smuosca) at the base of the murous, glads, muscular tunic, and the serous tunic, facing the celomic cavity. (After Young, The Life of Mammals, Oxford University Press.)

importance, secreting a series of enzymes in numerous small glands embedded in its walls and to some extent even in the surface epithelium itself. This epithelium, of simple columnar type, has, however, as its dominant function the absorption of the materials prepared from the food by the work of the digestive enzymes; once this epithelial wall is passed, they are discharged into the capillaries and lymphatics with which the intestine is richly supplied.

For efficient absorption, a larger area of intestinal epithelium is required than could be provided if the intestine were a straight smooth-walled tube. Methods of increasing this surface are effected by all vertebrates—particularly large forms, because of surface-volume relations between the absorptive surface and the bulk of body tissues for which food must be absorbed. Such increases of surface have been brought about by structural features on three levels of magnitude. (1) of microscopic size are countless small folds of the gut lining which appear to have been primitively a network of tiny ridges but in the higher vertebrates are generally in the form of countless small finger-like viilit (Figs. 257, 258). (2) In numerous instances there may be somewhat larger folds in which the submucous layer is involved as well as the epithelium (as in the mammalian folds of Kerkring, Fig. 257). (3) Major structural developments occur which greatly increase the area of the intestinal surface. Two are most notable: the spiral valve intestine characteristic of primitive vertebrates and the slender but long and highly coiled tubular intestine developed by teleosts and tetranods.

The Spiral Intestine (Figs. 18, p. 38; 24, p. 44; 251, A-E, p. 264). In members of every major group of fishes we meet with a type of intestine seemingly primitive for vertebrates-the spiral intestine. This is present in cyclostomes, on the one hand, and, on the other, is found in all bony fish types except the teleosts; it is, however, most characteristically developed in the sharklike fishes. There is in such forms no division of the intestine into "small" and "large" regions. Except for a short proximal tube connecting with the stomach and a short distal rectal region (where there may be an accessory gland which in sharks secretes sodium chloride), the entire length of the hindgut is occupied by the spiral intestine, a large, cigar-shaped body running fore-and-aft for most of the length of the abdomen. Its internal structure is complex; in addition to minor folds, its surface area is greatly increased by the presence of the spiral valve-a fold of epithelium and connective tissue extending in spiral fashion from one end of the intestine to the other, somewhat as if a carpenter's augur, or bit, were enclosed in a tube. In a minority of sharks the spiral valve has a different form which is, however, equally effective: the base of the valve twists but little and hence is relatively short; the valve fold, however, is highly developed and rolled up into a great scroll running lengthwise of the intestine. In either case, the surface area inside the gut is greatly increased.

THE INTESTINE IN HIGHER VERTERATES. Although among bony fishes the dipnoans and lower actinopterygians persistently keep the spiral valve structure, the teleosts, on the one hand, and land vertebrates as well, have abandoned it for a new type of hindgut structure in which the intestine is a slender tube without major internal folds (Figs. 251, F. p. 264, 252, p. 265), but which, in compensation, may be greatly elongated. In teleosts most of the length of the tube is a highly active digestive region, beyond which a short segment leads to the anus. A special teleost development is that of pyloric ecca—pouches, sometimes yn numerous, in the proximal end of the intestine into which food materials can enter and be absorbed

In both teleosts and land vertebrates there are enormous differences from form to form in the length of the intestinal tube and consequently in the area of absorptive surface. Two factors influence intestinal length: food habits and absolute size. Plant foods often include masses of complex carbohydrates which are difficult to digest and absorb, and hence the intestine is in general longer in herbivores than in flesh eaters. As regards the differences due to size of the animal, we encounter here again the question of volume-surface relationships. With increasing size, the volume of the body requiring nutriment increases faster than does the intestinal surface, and disproportionate elongation of the intestine is necessary to keep the absorptive surface in line with the demands made on it. From teleosts to mammals, small flesh eaters tend to have the shortest intestines, large herbivores the longest.

No trace of the spiral valve persists in any tetrapod, and the greater part of the hindgut universally consists of a slender, small intestine, coiled to a variable degree-in general more complexly so in birds and mammals than in the lower classes. This is the major seat of digestion and absorption. In some cases (as in man) subdivisions may be named, but the differences between them are very slight. Beyond the small intestine there is usually, in lower tetrapods, a short but broader segment which appears to be homologous, at least in a broad sense, with the colon, or large intestine, which is a highly developed terminal area of the gut in mammals. There is frequently a small outpocketing at the proximal end of the colon in lower tetrapods. In mammals this becomes the variably developed cecum, which in man and various other forms terminates in the vermiform appendix. The appendix is sometimes claimed to have evolutionary significance; but this does not seem to be the case, and its major importance would appear to be in the financial support of the surgical profession. The colon, when well developed, is not merely a place for the collection of feces pending evacuation, but a terminal digestive area where bacteria, plentifully present in colon and cecum, may make a final attack on cellulose or other difficult carbohydrates and a certain amount of absorption of water and other materials takes place. In lower tetrapods and birds the intestine opens distally into the cloaca; in typical mammals the short rectum, leading to the anus, is derived from the embryonic cloaca.

The Liver. In concluding this chapter we treat of two organs, liver and pancreas, derived embryologically from the gut endoderm, which are important both for secretions which they furnish to the intestine and for their functions in the metabolism of food already discested.

Amphioxus (Fig. 4, p. 15) has a sac-like outgrowth of the gut which is similar in position to the liver but of dubious homology; a large liver is, however, universally present in all true vertebrates. As shown by its embryonic history, it de-

Fig. 259. Diagram of an early stage of liver development to show the relationship of the ducts.



velops as an outpocketing of the gut below the stomach; it begins its development in the ventral mesentery, extends forward to attach to the transverse septum behind the heart, and then expands backward into the abdominal cavity. It has no constant form, and needs none, for its proper functioning rests on an appropriate internal arrangement and sufficient bulk. In general, we have noted, the endoderm forms only the thin lining of the gut tube and the gut glands; only in the liver (and to a lesser extent in the pancreas) does endodermal material bulk large in body composition.

Primitively, it would seem, the liver was evolved from a gland, and in its even the proposed of the proposed seems of the proposed s

The major duties of the multitudinous liver cells, however, are not those directly connected with digestion but with the treatment of food materials after their digestion and absorption into the body. In part its activity is that of a storage depot, particularly for carbohydrate storage as glycogen. Further, the liver cells act as complex chemical retoras which benefit the body as a whole; proteins may be synthesized here, fats altered in composition, proteins and fats transformed into carbohydrates, nitrogenous wastes such as ammonia transformed into less harm-

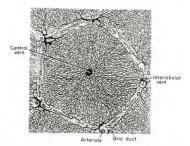
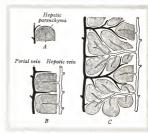


Fig. 260. Section of a mammalian liver, showing a lobule and portions of others. The portal system of virus has been injected (labeck), showing the course of the blood from interlobular virus rica a multituded simuosida through the sheets of liver cells to extent views of the lobels branches of the hole duct and of the hepatic artery are seen in the interlobular septa. (After Young, The Life of Mammals, Oxford University Press.)

Fig. 261. Diagrams to show the development of liver lobules. Masses of liver tissue (parenchyma) become clustered about branches of the excurrent hepatic vein; the portal vein branches (and those of the hepatic artery and bile duct, not shown) ramify external to the developing lobules. (From Arev. after Mall.)



ful substances such as urea or uric acid. For its major functions as atorage depot and manufacturing plant, the liver is strategically situated along a "main line" of the circulatory system. As will be described later (cf. pp. 326–328), all the food-carrying veins from the intestine collect as a hepatic portal system which filters through the liver tissues in a series of sinusoids before reaching the general body circulation. From these small vessels the liver cells thus have the first opportunity to select for storage or modification food materials newly arrived in the body.

Because of the dominance of metabolic over secretory functions, the structural arrangement of the liver is based on its relations to blood vessels rather than secretory ducts. A common pattern is that seen in Figure 260, and in a diagrammatic picture of embryonic development in Figure 261. The tissues are arranged in masses termed lobules, each has a central vien which carries blood to the hepatic veins and heart. External to the lobules (in addition to bile duct branches and arterioles) are vein branches from the portal system. Running inward, concentrically, toward each central vein are numerous sinusoids. The liver tissue between the sinusoids has the appearance of strands or cords of cells. Actually, however, these apparent cords are cut sections of plates of cells (Fig. 262) lying in a tangled network around the sinusoids. At the thickes, these plates are generally but two cells thick, so that every cell faces a sinusoid on one side or the other; in mammals they are but one cell thick.

Fig. 262. Diagrammatic enlargements of a small perion of a liver lobule (such as is shown in Fig. 269) to show the structure of the plates of liver cells. The plates are sparsed and perforated by channels which in life are occupied by simusoids. Left, typical structure in a lower vertebrate; the plates are in general two cells thick. Right, mammalian structure: the plates are in general one cell in thickness, (After Elias.)



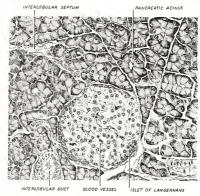


Fig. 263. A section through the pancreas of a rat, to show both exocrine tissue (pancreatic acini) and a pancreatic island. A duet of the exocrine part of the gland and a connective tissue septum between lobes are also shown. (From Turner.)

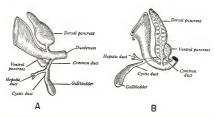


Fig. 264. Diagrams showing two stages in the development of the human pancreas. A, An early stage, with both dorsal and (smaller) ventral pancreas developing. B, Later stage in which dorsal and ventral portions are beginning to fuse. (After Arev.)

The Paucreas (Figs. 263, 264). Although, as we have seen, the intestine still produces in its walls (or in small and closely associated glands) certain of the enzymes utilized in digestion, much of the seat of enzyme production was transferred early in vertebrate history (with resulting greater efficiency) to a major external site, the pancreas. Stages in this transfer can be seen in Amphitous and cyclostomes. In the former there is no indication of a formed pancreas, but certain cells near the anterior end of the gat tube have the characteristics of pancreas cells. In the lamprey these cells form clusters of small glands in this same region. In most other vertebrates the pancreas is a discrete (if somewhat amorphous) structure external to the intestine, lying in the dorsal mesentery. But even when well developed, the pancreas appears to form in many cases as several or more separate outgrowths from the intestine (as, for example, in man, Fig. 264), and as a result of this multiple origin there tends to be considerable variation in the number and position of pancreatic duets.

The prominent function of the pancreas is that of an exocrine gland, which produces and pours into the intestine a series of enzymes (or rather proeuzymes) which act upon all three major types of food materials and are responsible for a great part of the digestive activities of the gut. In addition, however, sections of the gland are endocrine in nature, as discussed in Chapter 13.

### 13

# EXCRETORY AND REPRODUCTIVE SYSTEMS

From a functional point of view, a joint consideration of urinary and genital systems seems absurd, for excretion and reproduction have nothing in common. Morphologically, however, the two systems are closely associated and it is impossible to describe one without numerous cross references to the other. This association appears to be due to embryonic propinquity; the major organs of the two systems arise in areas of the mesoderm which lie close to one another in the walls of the trunk near the upper rim of the celomic cavity (Fig. 279, p. 291).

#### URINARY ORGANS

Kidney Tubule Structure and Function. Paired kidneys, developed in varied form in all vertebrates, are the major organs of the urinary system. The basic kidney structure is the minute kidney tubule or nephrom; the numerous tubules connect with a duct system which eventually leads, posteriorly, to the body surface.

Among vertebrates as a whole the most generalized type of tubule is that shown diagrammatically in Figure 265. 4, such tubules are present in forms as diverse as sharks, fresh-water and many marine teleoats, and amphibians. The proximal part is the spherical renal corpuscle. Its interior is a glomentus, a compact cluster of blood vessels comparable to capillaries (Fig. 266). The outer part, the capsule, is a double-layered hemisphere which forms the proximal end of the tubule proper; its inner surface is in close contact with the walls of the blood vessels of the enclosed glomerulus. Its cavity is continued by that of the contact under dubule, "along whose walls lies a network of capillary vessels; distinct proximate dubules," along whose walls lies a network of capillary vessels; distinct proximate in the contact was the contact with the contact when the contact was the contact with the contact when the contact was the contact with the contact when the contact was the contact with the contact when the contact was the contact with the contact was the contact with the contact when the contact was the contact with the contact when the contact was the contact with the contact was the contact with the contact when the contact was the contact when the contact when the contact was the contact when the con

\* Note that the term "fubule" is generally used in two ways: (1) as a synonym of nephron, i.e., a need to the entire nephric unit of renal corpuscle and convoluted tubule; and (2), more properly but more narrowly, for the latter structure only.

mal and distal sections of a tubule can usually be distinguished. Distally each tubule connects, in a fashion which varies in different groups, to ducts leading to the exterior of the body.

The result of nephron activity is the production of urine, destined for excretion and derived, obviously, from the associated circulatory vessels. Urine is composed mainly of water but contains in solution other substances, such as various salts and, particularly, nitrogenous wastes, most generally in the form of urea or uric acid. The functions served are twofold: (1) elimination of waste and (2) regulation of the internal environment.

Of the materials produced by the destructive metabolic process of the cells, those resulting from breakdown of carbohydrates and fats consist mainly of carbon dioxide and water, disposal of these presents no serious problem. Proteins, however, contain nitrogen, and their residues include simple nitrogenous compounds, particularly ammonia, which are toxic to the animal. They are generally transformed rapidly in the liver into relatively harmless urea or uric acid, but even so, their removal is necessary, for this the kidneys bear the major responsibility, as they do for removing other harmful products which may be present in the body.

In Chapter 4 we pointed out the necessity of maintaining the body cells in a proper environment, including the presence, in solution in the fluids bathing them, of appropriate amounts of specific simple salts. The maintenance of proper salt content demands a balance between intake (mainly via the intesting) and out-put. Excess salt intake requires excretory devices, particularly the kidney tubule; low salt content of the blood requires removal of excess amounts of water, likewise attainable through the work of the kidney.

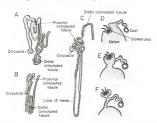


Fig. 26.5. Tabule types. A to C. The three major types common in shall vertebrates. A, Presumshly the most primitive, with corpused og good size, found in elassmearanth, fresh-scarte bong tibers, amphibians. B, Corpusch reduced or absent, characteristic of sall-water telesust, regilies. C, Grapusch larger a loop of Herle interrectly found in manumals, birds. D to F, Frimitive halled types found in lower telestrates, principally in the embryo, and perhaps illustrating the early evolution of kidney tabules. D, Special small colorism chamber and generation, if present in colons, not associated with tables. D, Special small colorism chamber and generation of the present in colons, not associated with tables. D, Special small colorism chambers and generation of the present in colons, and sascincided with tables. The colorism constraints of the proposed colorism of the proposed colorism of the proposed colorism of the colorism of the proposed colorism of the proposed colorism of the colorism of the proposed colorism of the colorism of the proposed colorism of t

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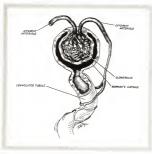


Fig. 266. A mammalian renal corpuscle. Here the vessels around the tubule come from the arteriole; in animals with a renal portal circulation, capillaries from this system surround the tube instead. (After Turner.)

The way in which a kidney functions is today fairly clear. Two distinct operations are present, one having to do with the renal corpuscle, the other with the tubule proper. The structure of the corpuscle suggests that we are dealing with a filtering device which draws off a filtrate from the blood plasma. This is indeed the case, as shown by liquid drawn from the capsule by micropipette in amphibians. Blood corpuscles and large protein molecules do not pass the filter amphibians. Blood corpuscles and large protein molecules do not pass the filter that otherwise the filtrate includes all blood contents, including not only water and wastes but also valuable food materials—particularly glucose. Further, the quantity of liquid filtered is excessive. It has been calculated that if all the liquid passed through a frog's glomeruli were actually eliminated from the body, nearly a pint of urine would be produced daily by this small animal, and a man would produce about 50 gallons!

Obviously, nothing of the sort happens. This excessive activity of the renal corpuscle is counteracted by the work of the convoluted tubule. There is a certain amount of excretion of waste substances from tubule cells into the urine as it passes by. The main tubule function, however, is to resorts, selectively, much of the filtrate; this includes much of the water (otherwise the animal would be rapidly dehydrated), but includes especially recapture of valuable materials, particularly glucose and salts, leaving the urine contents mainly water and nitrogenous wastes.

In a nephron the crude work is, so to speak, done by filtration from the glomerulus; the tubule proper adds the necessary refinement to the process.

Tubule Types and Vertebrate History. Whether fresh or sall water formed the original vertebrate home has been a problem of interest to students of kidney function as well as students of classification and phylogeny. The fossil record strongly suggests that the earliest fishes dwelt in fresh waters and only later invaded the seas. A study of kidney tubule structure and function leads to the same conclusion.

Three types of nephric units may be found in the adult kidney of one group

or another (Figs. 265, 267). (a) In one type (Fig. 265, A), found characteristically developed in such varied forms as amphibians, fresh-water bony fishes and elasmobranchs, there is a renal corpuscle of good size, and hence a high water output. (b) A second type (Fig. 265, B) is that found in many marine teleosts and in reptiles; the corpuscle is small or absent, and hence water output is low. (c) A third type (Fig. 265, C) is that seen in mammals, and, in a less extreme form, in birds. The glomerulus is large, but there is interjected into the middle of the convoluted tubule a long slim extra segment, the loop of Henle. This type of tubule appears to be a powerful resorbant of water, and hence despite a plentiful output at the glomerulus, relatively little water reaches the bladder.

From the distribution of these tubule types among vertebrates a consistent story can be constructed regarding the environmental history of vertebrates. It is assumed that type (a) is the primitive tubule, possessed by early freah-water vertebrates and retained by forms which still inhabit such waters. Such an animal lives in a medium more dilute than its own body fluids, and hence is in danger of overdilution of these fluids (and consequent death) by osmosis on body and gut surfaces. To prevent this, large amounts of water must be eliminated, and this is afforded by the presence of a large corpusche. If, on the other hand, a fish enters the sea, it is liable to dehydration because of the greater salinity of the surrounding medium. Water must be conserved and much salt eliminated. In marine teleosis, the glomentia are frequently reduced or absent and water output consequently reduced; further, salts and wastes are excreted by the cells of the gill membranes as well as by the kidneys.

Land vertebrates, living in a dry environment, have much the same prob-

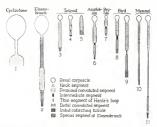


Fig. 267. Diagram of kidney tabules of unious vertebrates, all reduced on the same scale, to show the relative size of the components in the different groups. The glomesuli are at the upper end necesse, and the tubules are represented as if straightened out. The glomesuli are well developed in most case, and the tubules are represented as if straightened out. The glomesuli are well developed in most groups and of encomous size in cyclostomes and elamostenes, but of reduced dimensions in repities, and are done away with in some marine teleoasts (5). All have a proximal convoluted segment of the buddles an intermediate segment, followed by a distal convoluted tubules, appear in some fishes and is present in all land forms. The intermediate segment feedomes the loop of Henle in birds (in part) and ammunity, this loop may be much elongated in the latter group, 1. Higafick, 2. skate 3, scalipst, of sish 5, toadfish; 6, frog; 7, painted turtle; 8 and 9, chicken; 10 and 11, rabbit. (After Marshall, Kepton, from Prossery.)

lems as a marine fish. Water must be conserved. In modern reptiles this is accomplished by reduction in size of the renal corpuscles with a consequent decrease in water output. Birds and mammals have developed a different method of conservation. There is a normal glomerulus of large size and consequent high water output. The complex tubule, however, is an "Indian giver" and the presence of the loop of Henle results in absorption of much of the water, the product is a relatively concentrated urine.

The reasonable argument above leads to the conclusion that the presence of a large glomerulus is a primitive character, due to the need for an efficient water pump in a vertebrate living in fresh water. But one could still, thus far, advocate vertebrate origin in the seas; it could be suggested that the ancestral form was a marine fish, which had only a small glomerulus, and that the development of a large glomerulus came later, with a move into fresh water. And a further fact seemingly inconsistent with the argument for fresh-water origin is that the sharks have a large glomerulus and yet are marine!

It is the sharks, however, which clinch the argument for fresh water. The shark lives in a medium with a higher salt concentration than his body fluids, yet pumps water out through his large glomeruli with as little concern as a freshwater fish. He can do this without the danger of water loss through osmosis, for (in addition to salt climination through a rectal gland) the shark has attained an osmotic pressure of his internal fluids equal to, or a bit higher than that of set water without increase of his salt concentration. This is accomplished in pedial fashion by his retention in the blood stream, without apparent harm, of a large amount of urea, which raises the total concentration of materials in solution. We have thus in sharks and in salt-water teleosts two radically different kidney adaptations to salt water, this indicates that the two groups entered the seas independently, adapting themselves to the new environment in very different ways.

Primitive Tubule Structures. The types of nephric units described above are those most characteristic of adult vertebrate kidneys. There are, however, other patterns which are more often found in embryos than in adults, particularly in the first units developed, and more often in lower than in higher vertebrates; there is hence ample reason to consider them primitive in nature. In these types (Fig. 265, D-F) there is always a ciliated funnel opening from the colomic cavity into the tubule: a typical glomeralus is sometimes persent, but some cases the glomerulus lies in the celomic cavity, and in still other cases it is absent altogether. Originally kidney tubules may have simply drained excess fluid and accumulated waste from the celomic cavities; the development of a glomerulus and its incorporation in the tubule was perhaps a later development.

Most invertebrate groups, and even the chordate Amphioxus have excretory structures of somewhat varied nature termed nephridia. These, however, are not homologous to the vertebrate nephron, which appears to have evolved independently, mainly as a water "pump" for life in fresh waters. Not improbably nephridia were present in ancestors of the vertebrates, as they are in Amphioxus. But with the "invention" of the vertebrate kidney tubule, which could take care of wastes in addition to its major function of water climination, nephridia, if present, would be redundant and could be abandoned.

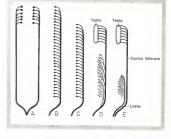
Organization of the Kidney System. So far we have discussed merely the nature of the microscopic kidney units. Now to be considered is the organization of these secretory units and the duct systems leading from them to form the gross structures of the urinary system. As seen in most vertebrates, the pattern of the kidney system appears fairly uniform, with paired, compact kidneys projecting into the abdominal cavity from its dorsal walls and paired ducts leading from them which often empty into a median bladder. Study, however, shows that there are basic differences from group to group, kidneys, ducts and bladder are varied in nature and structure.

These variations have two major causes. (1) Unlike most body organs, the kinder must begin to function at an early stage to take care of embryonic wastes; hence there must be rapidly developed a functioning embryonic kidney which, however, may be subject to modification or replacement in later embryonic and adult stages. (2) The genital organs lie adjacent to the kidneys, and—the testis particularly—tend to "invade" the urinary system, taking over part of its tubes and ducts for their products and in consequence causing marked modifications of the urinary organs.

We may begin our discussion of kidney organization by the description of the structure and development of an "idealized" primitive kidney which may be termed a holonephros. In our embryologic story we have noted the presence in the mesoderm on either flank of a band of kidney-forming tissue lying between the somites and the lateral plate, and frequently showing segmental division into a series of small nephrotomes (Figs. 62, D, p. 97: 67, C, p. 104; 269). Probably in the ancestral vertebrate each nephrotome gave rise to a single renal tubule. As with the somites, the differentiation of nephrotomes takes place in the embryo from before backward, the oldest members of the tubule series being those at the front end, the last formed at the posterior end of the trunk.

In the embryo a longitudinal duct soon develops on either side, gathering the urine from the series of segmentally arranged units; the two ducts often unite before emptying to the exterior in the region of the cloaca. This primitive kidney duct is here termed the archinephric duct.\* The duct, like the tubules, is of meso-

Fig. 268. Diagrams of kidney types. A, Pronephros (embryonic); B, theoretical holonephros (each trunk segment with a single tubule), much as in a young hagfish or apodous amphibian; C. primitive opisthonephros: pronephros reduced or specialized, tubules segmentally arranged, as in hagfish. D, Typical opisthonephros; multiplication of tubules in posterior segments, testis usually taking over anterior part of system, trend for development of additional kidney ducts (most anamniotes), E. Metanephros of amniotes: an opisthonephros with a single additional duct, the ureter, draining all tubules. In A, both sides of the body are included; in B to E, one side only (cf. Fig. 288).



<sup>\*</sup> Wolffian duct, pronephric duct, mesonephric duct are all terms applied to this same duct at different developmental stages.

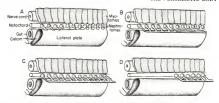


Fig. 269. Diagrams of the anterior part of the trank of an embryo (skin removed) to show the de-dopment of the archinephric dark. A Most anterior-proceptive—embryomens are building out tubules which tend to fuse posteriorir. B, The pronephric buildes have formed the dark some of the properties that the proceptive that the proceptive through the posteriority are forming tubules which are to centre the dark. C, The more posterior tubules have joined the dark. D. The pronephree lost, but the archinephric dark formed by it persists to drain the more posterior part of the kidner,

dermal origin. Generally it originates by a fusion of the tips of the most anterior and first-formed nephric units (Figs. 268, A, 269, A, B). It grows backward along the lateral surface of the nephrotomes (or the band of nephrogenic tissue), and as tubules develop farther back they grow outward to connect with it (Fig. 269. C). The end result, ideally, is a holonephrox a kidney with a single nephric tubule in each trunk segment on either side of the body, the series draining through a pair of architephric dutes (Fig. 268, B).

Such an ideal holomephros is found only in the larvae of hagfishes and apodous amphibians. In adults of even the lowest of living vertebrates the most anterior and first-formed part of the kidney tubule system is specialized and degenerate. These anterior tubules are called the pronephros (Figs. 268, 4, 269, in one fashion or another, the kidney of adult living vertebrates, may be termed as a whole the opishonephros, the "back kidney" (Fig. 268, C, D). This opisthonephros generally differs from the theoretic holonephros in three main particulars: (1) The anterior tubules (pronephros) are eliminated. (2) Above the hagfish level the simple segmental arrangement is lost; a variable (and often high) number of tubules may develop for each segment. (3) In most vertebrate groups the archinephric duct is used for sperm transport and a new urinary duct may develop.

Amniote Kidney Development. To show an extreme contrast with the ideal holonephors we will depart from a logical sequence and describe the development of the kidney in an amniote—specifically, a mammal. In mammals, as the mesoderm is undergoing differentiation, a short series of tubules at the back end of the head and future neck region form as the pronephros, and in connection with them there develops an archinephric duct which grows rapidly back to the cloacal region (Fig. 270, A). These tubules function only briefly and the degenerate. Meanwhile, however, differentiation of tubules has continued back ward without interruption to form a second embryonic nephric structure, the mesonephros (Fig. 270, B), which functions for much of the period of embryonic life in mammals and may persist until after brith in reptiles. The pronephric tu-

bules are often rudimentary and without glomeruli; typical mesonephric elements are, in contrast, well formed. At first they are metameric in arrangement, but multiplication of tubules later takes place and the segmental condition is obscured.

As development continues, the mesonephiric kidney degenerates in turn and its place is taken functionally by a metanephros, the functional kidney of the late embryo and mature mammal. This arises (Fig. 270, C. D) from the most posterior part of the nephrogenic tissue (king. 270, C. D) from the most posterior part of the nephrogenic tissue, which forms a compact mass in the roof of the lumbar region of the body case, which forms a compact mass in the roof of the turnbar region of the body case, the compact has a compact mass in the roof of the lumbar region of the body case, and the surface of the roof of the lumbar region in the archive part of the roof of the lumbar region of the roof of the

We see in this story the development in the amniote embryo of three successive kidney structures—pronephros, mesonephros, metanephros. It is often stated or implied that these three are distinct kidneys which have succeeded one another phylogenetically as they do embryologically. Upon consideration, however, it will be seen that there is no strong reason to believe this. The difference are readily explainable on functional grounds; the three appear to be regionally specialized parts of the original holonephros, which serve different functions.

The pronephric tubules are variable and often rudimentary in nature, but there is no sharp structural break between them and the mesone-phric tubules which immediately succeed them. Their one distinctive feature is that there here forms the archinephric duct. But there is nothing really significant or mysterious about this; it is a practical matter. Once the first tubules are formed they begin

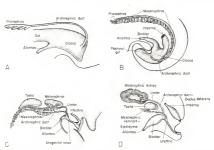


Fig. 270. Diagrams to show formation of the metanephros of an amiote (male) embryo as seen from the left side. A, Pronephros and duct formed; B, mesonephros partly formed; C, pronephros reduced, posterior part of mesonephros functional, ureter formed, and metanephros beginning to differentiate; D, definitive stage; mesonephros reduced, and tubules and duct utilized only for sperm transport; metanephros the functional kidney.

to function. The formation of a urinary duct cannot wait until the entire kidney is formed; the anterior tubules just cannot wait that long!

In amniotes mesonephros and metanephros are readily distinguished. The latter is vastly greater in size and is served by a distinct duct. But it is, after all, derived from a part, even if a greatly expanded part, of the same band of tissue that forms, more anteriorly, the pronephros and mesonephros; the development of a distinct duct is presumably due to the impossibility of all of the multitude of tubules formed in this tissue draining directly into the archinephric duct (as well as to the fact that the old duct is used for sperm transport). Both mesonephros and metanephros are portions of the opisithonephros; the former is developed rapidly to function in the embryo during the period of the necessarily slower formation of the complex metanephros.

Head Kidney. In sharklike fishes and amniotes, the pronephros is an exceedingly short-lived structure. In contrast are conditions in other fishes and in amphibians (with small-yolked eggs) in which the embryo of necessity becomes an active food-seeking larva at an early stage. In such larvae the pronephros persists to satisfy excretory needs; it is, however, highly specialized and is frequently termed a head kidney, in reference to its anterior position. The number of tubules forming in its generally reduced to but one to three large convoluted tubules which frequently function in jointly draining liquids from a single large glomeulus situated in a special pocket of the celonic cavity. This larval head kidney usually disappears in the adult (and is commonly represented by a mass of lymphoid tissue) but persists throughout life in hagsibes and many teleosts.

The Opisthonephros of Anamniotes (Figs. 271, 272, 273). In lower vertebrates the distinction between mesonephric and metanephric portions of the

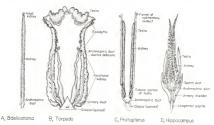


Fig. 271. Urogenital systems in ventral view of males of A, the slime hag. Belelostoms: B, the elasmontance Torpolos, C, the laughds Producture: D, a between the scattered Hippocampus. In A the testis, not shown, is pendent from a mesentery lying the table kink kinkeys and has no connections, when  $\ln B$  the testis has appropriated the statemer part of the kink had the same has no made in land vertebrates, and utilizes the entire length of the architechric size approach of the C the testis duck drains, on the contrary, only into the posterior part of the kinkeys and thence to the terilinelysis duck in D the sperm duct is entirely independent of the kinkey system. (4 after Concle B after Borecut Cather Kerr, Parker: D after E blancks.)

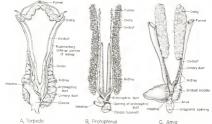


Fig. 2.72. Urogenital systems in ventral view of females of A, the clasmobranch Torpedo; B, the lungtish Protopterus; and C, the primitive actinopterygian Amia. (In Torpedo the shell gland is not developed.) (A after Borcae, B after Parker, Kerr, C after Hyrd, Goodrich.)

kidney is never as distinct as in amniotes, and the entire structure is best termed an opisthonephros. In hagfishes the structure is a very simple one; the long slenior kidney has a small number of tubules arranged in essentially segmental fashion the length of the trunk, and all are drained directly by the archinephric duet (Fig. 268,  $C_c$  271,  $A_c$  277,  $A_c$ ). Lampreys are similar in kidney build except that the tubules are somewhat more numerous. In bony fishes the number of tubules may increase, but drainage is still directly by the original duct and the kidney is generally a long and slender structure (Figs. 271,  $C_c$   $D_c$  277,  $C_c$   $D_c$  278,  $D_c$  277,  $C_c$   $D_c$  277,  $C_c$   $D_c$  278,  $D_c$  277,  $C_c$   $D_c$  278,  $D_c$  277,  $D_c$  278,  $D_c$  277,  $D_c$  278,  $D_c$  277,  $D_c$ 

In other anamiotes, however, the structure is more complex (Figs. 268, D, 2718, 272, 4, 273, 277, C, D). The front part of the elongate opisthonephros tends to be reduced, while posteriorly it becomes generally much expanded, with a great multiplication of tubules, thus foreshadowing the anmiote condition. Part Office is, further, an approach to the amniote condition in the duct system. Part of the urinary drainage may still be by way of the archinephric duct, but there is a strong trend in sharklike hisse and amphibians for the development of separate ducts which foreshadow the anniote development of a ureter and tend to leave the old duct free for sperm transport in the male.

The Anniote Kidney. As is indicated by this review of the phylogenetic development of the kidney in lower vertebrates and by our earlier description of mammalian development, the amniote kidney is a specialized end type in which the trend toward posterior concentration and toward development of a new duct system has attained a peak development with the formation of a definitive ureter. The anterior part of the old opisthonephros functions only in the embryot the adult kidney is formed by a great expansion of the nephric itsue toward the back of the trunk (cf. Figs. 268, E. 277, E). In reptiles (Fig. 274) the metanephroj, often cremulated in appearance, contain in lizards a number of kidney tubules

<sup>\*</sup> Frogs are here (as often) exceptional, for in correlation with the greatly shortened body, the whole kidney is a short, compact structure.

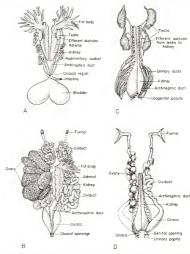


Fig. 273. Urogenital system of amphibians. A, B, Male and framale organs of a frog (Rana); nB the ovary (show only on the right side of the body) is in a condition close to breeding maturity, B bladder and intestine are not shown in B C, B, Male and female organs of the wroded Salamanira, like bladder and intestine are not shown in B C, B, Male and female organs of the wroded Salamanira, like C the urinary dots to the right side are detached and spread out to show their connections which the kidders, B of the overall B and B are the salamanical properties of B and B and B are the evident of the same side is partly removed to show the more protection urinary detacts. Ventral views, C (A and B after B-B-B-B).

estimated in various forms to be from 3,000 to 30,000. In birds (Fig. 275) the kidney, likewise typically lobulated, contains a much larger number of tubules, some 200,000 in a fowl, for example; this is presumably correlated with the greater metabolic activity of birds and a consequent increase in need for waste disposal. In mammals the tubule count is likewise high; a mouse appears to have about 20,000, and in such large mammals as a man or cow the number may run into the millions.

The mammalian kidney (Fig. 276) is a compact structure, frequently beanshaped, with a cavity, the hilus, through which blood vessels and ureter enter.

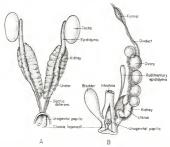


Fig. 274. Urogenital organs in reptiles. A, Male organs of the lizard Varanus. B, Female organs of Sphenodon. In A the bladder is omitted; in B it is shown turned to one side. In B the organs of the left side only are figured. Ventral views. (A after Vanderboeck; B after Osawa.)

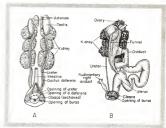


Fig. 275. Urogenital organs of pigeon; A. male; B. female. The burss (of Fabricius) is a pouch, of uncertain function, opening dorsally into the cloaca of birds. (A after Röseler and Lamprecht; B after Parker.)

Within the kidney the ureter expands to form a renal pelvis, sometimes subdivides into a series of calyces into which collecting tubules drain. In section the kidney usually shows distinct "rind" and "marrow"—cotrical and medullary portions, the former including glomeruli and convoluted tubules, the latter (striated in appearance) containing the loops of Henle and the collecting tubules.

We may parenthetically note here the nature of the blood supply to the kidney. The major filtration function, performed by the glomeruli, has in all cases a 288 THE VERTERRATE BODY

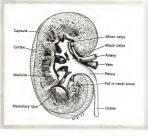


Fig. 276. Section through a mammalian kidney. (From Windle, Textbook of Histology, The McGraw-Hill Company.)

blood supply furnished by branches of the aorta. In cyclostomes, on the one hand, and mammals, on the other, the entire blood supply to the kidney is arterial. In all intermediate groups, however, from jawed fishes to reptiles and, to a very slight degree, in birds, we find an accessory blood supply in the renal portal system (cf. p. 330). Venous blood in its course to the heart from the tail or hind legs, or both, is forced to pass through a venous capillary system within the kidney which bathes the convoluted tubules, but is never concerned with the glomeruli.

Evolution of Urinary Ducts (Figs. 277, 288, p. 299). In the primitive vertebrate kidney, as seen in cyclostomes, a pair of simple archinephric ducts suffices for the drainage of urine. In cyclostomes both sperm and eggs are shed freely into the abdominal cavity on their way to the exterior. In gnathostomes, however, the sperm tubules come into connection with kidney tubules and utilize the original kidney duct as a passage. In a few modern vertebrates—the Australian lungfish, lower actinopterygians, the common frog and a few other amphibians—this duct serves equally for sperm and urine conduction. In general, however, this awkward dual function is unsatisfactory, and there appears to have been (so to speak) a struggle between urinary and genital systems for possession of the archinenhric duct.

Among bony fishes the urinary system has been the winner. In African and South American lungfishes and Polyterus (Fig. 277, F; cf. Fig. 271, C, p. 284; Fig. 288, c, p. 299) sperm enter the kidney duct, but only near its posterior end; in teleosts there has developed a quite separate tube for sperm conduction and the archinephric duct is restored to its original urinary function (Fig. 277, G; cf. Fig. 271, D, p. 284; 288, d, p. 299).

In all other gnathostomes the fight has gone the other way. The archinephric duct has been taken over in the male sex for sperm conduction and there is a development, partial or complete, of new ducts to care for the drainage of urine. In Figure 277, C-D, are shown diagrammatically stages in this process as seen in elasmobranehs, on the one hand, and amphibians, on the other. In both groups (as might be expected) development of new urinary ducts progresses more slowly,

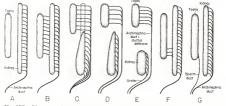


Fig. 277. Diagrams to show the differentiation of urinary and genital ducts in the males of various vertebrates. Ventral views, left side only shown. A, Condition seen in cyclostomes; archinephric duct solely for urinary system; gonad not involved. B. Condition presumably primitive for gnathostomes, preserved in the sturgeon and gar pike. Testis connects at various points with kidney and thence with archinephric duct. C, Stage beyond B as seen in many sharks and urodeles. The testis has taken over the anterior part of the original kidney; the functional posterior part of the opisthonephros tends to drain by a series of ureter-like ducts. D. Stage more advanced toward the amniote condition, found in some sharks and urodeles; the kidney drainage is by a single ureter-like duct. In females (not shown) of the types represented by males in C and D, the tendency toward development of new ducts for kidney drainage is generally not so marked as in the males; the condition shown in D is reached by few female forms below the amniote level. E, Amniote condition; a definite single ureter formed in both sexes. F and G, Lungfish and a teleost, showing a type of specialization peculiar to modern bony fishes. The testis tends to concentrate its connections toward the back end of the kidney (as in F), and in teleosts evolves a separate sperm duct, releasing the archinephric duct for its original urinary functions. Note that the two ducts for sperm and urine in G are not respectively homologous with ductus deferens and ureter, as might be thought at first sight,

phylogenetically, in females, where no competition exists, than in males. A first stage in differentiation is one in which there develop short urinary collecting tubes which empty into the posterior part of the archinephric duct. Beyond this, in many amphibians and female sharks, there is a stage in which the more posterior of these urinary tubes run separately to the closac but the more anterior one still drain into the old duct. A final development, attained in male sharks and, in parallel fashion, in a few male amphibians, is one in which all ducts from the kidney unite to form a single duct leading independently to the closca, leaving the archinephric duct free for sperm transport. There is thus attained the development of a new urinary duct comparable to the ureter, which we have previously described as the functional duct in the higher, aminote, verbarted calesses.

Urinary Bladders. In a majority of vertebrates there is developed a bladder of some sort, a distensible sac in which urine may be stored. In female elasmobranchs and in some of the more primitive bony fishes (Figs. 272, C, 293, D, E) a small urinary bladder may develop from the conjoined posterior ends of the archinephric ducts themselves, or at the posterior end of each duct. In male elasmobranchs the archinephric ducts transport sperm, and no bladder develops along their course, but small bladder-like expansions may occur in the accessory urinary ducts developed in this group. In cyclostomes and in teleosts (Figs. 271, D, 293, A) a bladder may develop from a pinched-off portion of the cloaca.

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Fig. 278. Section of a mammalian bladder showing "transitional epihelium." The epithelium is shown as in a relaxed state, when the bladder is distended, this peculiar begot episterched and its thickness reduced to a third or so of that shown here. (From Windle, Texthook of Histtology, The McGraw-Hill Company.)

This last type of development is that which gives rise to the bladder of land overtebrates. In tetrapods a bladder is useful both as a rudimentary sanitary measure and in many cases (such as frogs and turtles) as a source from which water can be resorbed to counteract desiccation under terrestrial conditions. In amphibians and reptiles a bladder is prominently developed as an outgrowth from the floor of the cloaca (Figs. 273, A, 274, B, 294, A, p. 305); this often lacks a direct connection with the kidney ducts. Voiding of urine from the bladder takes place through the common cloacal outlet. In mammals the ureters come to enter directly into the bladder, so that no passage of urine through a cloacal cavity is necessary to reach it. Among reptiles the bladder is lost in some lizards, in snakes and in crocoditions, and, further, has disappeared in birds except in the ostrich. In its absence the urine is poured into the cloaca and may be mixed with the feecs. We have noted in an earlier chapter (p. 104) that the bladder plays an important part in amniote embryology, for the allantois, an important embryonic membrane, is elaborated as an outgrowth from the urinary bladder.

The tetrapod bladder is a highly distensible structure with stout walls endowed, particularly in mammals, with thick coats of smooth musculature. The lining is of a peculiar type, known (inappropriately) as transitional epithelium (Fig. 278). When the bladder is empty, this appears to be of a thick, stratified nature; when distended, it is capable of thinning down to a layer or two of flat squamous cells.

### GENITAL ORGANS

Sexual reproduction is universal in vertebrates and in almost every case the two sexes are functionally separate. The basic reproductive structures are the gonads—ovary or testis. In these organs are produced the gametes—eggs (ova) or sperm—by the union of which the new generation is initiated. In all gnathostomes there are associated with the gonads tubes or ducts for the transport of gametes and in certain cases for the protection and nourishment of growing young within the female body. In various groups copulatory organs, adding in internal

fertilization of the eggs, may develop, and secondary sexual characters frequently affect general body size or proportions or such features as the plumage of birds, the mammary glands of mammals, antlers and horus in ruminants.

Sex Development. The sex of an individual depends basically upon the nature of its chromosomal inheritance, a balance between male and female potentialities received from the two parents. As discussed in Chapter 5, the early development of the embryo is due mainly to the organization already present in the unfertilized egg, and the influence of the sperm and the hereditary characters which it introduces are not appreciable until a relatively late stage. In consequence, the early embryo has, so to speak, no knowledge of which sex it is to become and must be prepared for either possibility. We thus find that for some time the sex organs of the embryo remain in an indifferent stage, during which gonads and sex ducts proceed far in their development without showing indications of a trend specifically in either male or female direction (Figs. 279, C, 280). Eventually, there appears a definite sexual stage, presumably associated with the initiation of hormone secretion. The gonads become definitely testes or ovaries, and only the ducts and other accessory structures appropriate to one sex or the other continue their development. Nonpertinent structures of the opposite sex cease to grow and may be resorbed, but are sometimes merely arrested in their growth, to persist as rudiments in the adult.

The mechanisms of sex determination, however, are so delicately balanced

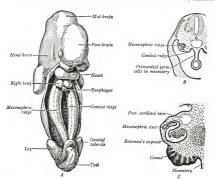


Fig. 279. A. Ventral dissection of a haman embryo of 9 mm, digestive tract removed, to show gonthal ridge and kilney (mesone-princ ridge) projecting downward into the (opened) eclosinic cavity, B, Cross section of an embryo at an earlier stage (7 mm.); and C, a slightly later one (10 mm.) for the primary sex cords are forming in the still "indifferent" gonad, and capsule and glomerulus are forming in the kinder bubles, (Fron Arcy.)

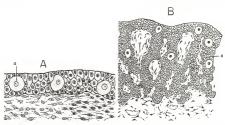


Fig. 280. Early stages in mammalian goand development. A. A section of the epithelium of the good at an early indifferent stage; primordial germ cells are present (a), has see cords are not developed. B, A somewhat later stage, with primary sex cords (a) growing inward from the epitheliul laver. (From Maximow and Bloom).

that in many vertebrates the gonads hesitate (so to speak) between the two possible alternatives, and both eggs and sperm may tend to develop. Only in very exceptional cases (the teleost families Serranidae and Sparidae) do both types of gametes come to maturity in the same individual at the same time of life, creating a functional hermaphrodite; but intersexual conditions of one sort or another are far from rare. A percentage of hagfishes remain sterile intersexes throughout life; in some amphibians (as the common frog genus Rana) individuals may be functional females when young but in old age shift to the male side of the halance and produce sperm.

Goniads. There is in vertebrates a great difference in the rapidity with which different organ systems develop. The nervous system, for example, grows very rapidly in early stages; the gential organs are, on the other hand, slowest of any to develop. This is correlated with the fact that whereas most bodily structures must be put to use at birth (or even earlier), the sex organs do not function until maturity of the individual has been takined.

The gonads make their appearance only at a stage when most of the other organ systems have been blocked out and the celomic cavities well developed. Paired longitudinal genital ridges form along the roof of the celom, medial to the embryonic kidneys and on either side of the dorsal mesentery (Fig. 279). Elongate to begin with, the gonads developed from such ridges often become relatively short and compact in later stages, with a usual trend for anterior concentration of tissue. The germinal epithelium of the ridge, continuous with the mesodermal lining of the rest of the celom, forms the more important structural elements of the gonad (Figs. 279, B. C. 280, A.; 281, A.); mesenchyme lying beneath the epithelium forms connective tissue and in higher vertebrates, at least, gives rise to special intertitual tissues which are believed to be a source of gonad hormones.

Before the end of the indifferent stage the gonad generally develops into a swollen structure, extending downward into the celomic cavity from its dorsal wall. From the germinal epithelium covering its surface, finger-like structures. the primary sex cords (Figs. 279, C; 280, B; 281, B), grow inward into the substance of the gonad. These cords contain, in addition to supporting elements, the germ cells from which eggs or sperm later develop.

It seems logical to assume that these germ cells arise locally, within the mesodermal epithelium of which they are a part, There is, however, a peculiar quirk in the story. A considerable body of evidence indicates that the first germ cells to appear in ovary or testis are actually derived from endoderm. In embryos of every vertebrate group from evclostomes to mammals there have been observed in the gut lining cells which histologically are quite distinct from the ordinary cells of the digestive tract. If a series of stages is followed through, these distinctive cells can be seen to leave the gut walls and migrate—either through the intervening tissues (Fig. 279, B) or by way of the blood stream—into the genital ridges, to become the primary germ cells. It is generally believed that they pro-

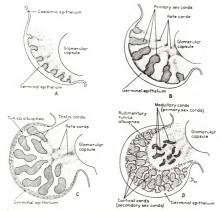


Fig. 281. Development of testis and ovary of a manual. A Cential ridge, with incipient primary sex cords growing inward from the premiumal epithelium to barge is alightly centrier has Figure 200. B. B. Cound still in the indifferent state, the primary sex consumers to the constraint of the primary sex consumers of the primary sex constant of the primary sex c

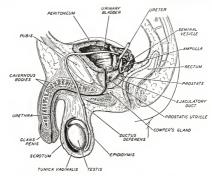


Fig. 282. Male reproductive organs in Homo. (From Turner, General Endocrinology.)

duce at least a first generation of eggs or sperm. Whether or not, however, they are the ultimate source of all the eggs or sperm produced during the life of the individual is uncertain, and it is possible that their function may be merely the initiation and stimulation of the process of gamete formation.

Biologists have often emphasized the fact that in animals in general the germ cells form an exceedingly independent tissue; the rest of the body is, from this point of view, merely a temporary structure shielding the potentially immortal germ plasm. In many invertebrates the future germ cells become distinct from the rest of the embryo at an early cleavage; the migration of vertebrate germ cells is, possibly, a demonstration of their equally distinctive nature.

Ovary: Egg Production (Figs. 284, 285). In the development of an ovary beyond the indifferent stage the primary sex cords degenerate and there is generally a proliferation inward of secondary sex cords (Fig. 281, D. p. 293). In these the ova arise from the germ cells after repeated divisions and by a complicated maturation process—the process of openesis. Each maturing egg cell may be surrounded by a cluster of other cells from the sex cords to form a follicle, and connective tissue cells may form a further external sheath. The follicle cells aid in the sustenance of the growing egg and are a seat of sex hormone formation. In forms with large-yolked eggs the follicle becomes relatively enormous, forming a major budge on the ovarian surface.

At seasons of reproductive activity, ripe follicles burst from the surface of the vary into the surrounding celomic space—the process of orulation. In most lower vertebrates the follicle is quickly resorbed, but in mammals and certain elasmobranchs it persists for some time, its cavity filled by a body of yellow ma-

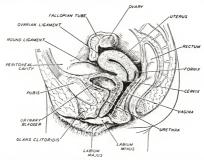


Fig. 283. Female reproductive organs in Homo. (From Turner, General Endocrinology.)

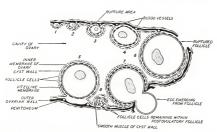


Fig. 284. Diagrammatic section through a lobe of the frog's ovary. I to 5 Illustrate stages in the growth of the follicle; 6 and 7, rupture of a follicle and emergence of egg; 8, postovulatory follicle. (From Turner).

terial—the corpus lateum, which secretes the hormone, progesterone (p. 418). The number of eggs in a mature state in the ovary at any one time is, in most groups, small—from two to a dozen in many cases. In amphibians, however, hundreds or even thousands of ripe eggs may be present at breeding time, and in 296 THE VERTEBRATE BODY

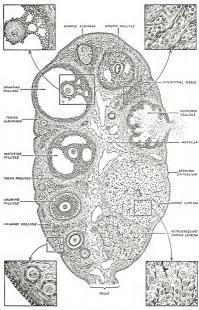


Fig. 285. Diagram of a composite mammalian ovary. Progressive stages in the differentiation of a follicle are indicated on the left. The mature follicle may ovulate and form a corpus lateum (right) or degenerate without ovulation (atteit follicle). (From Turner.)

teleosts there may be hundreds of thousands or even millions of tiny eggs (the codfish is estimated to lay 4,000,000 in one season).

The ovary is usually a paired structure, often with a simple oval shape in a resting phase but frequently distended and irregular in outline at the breeding season. In cyclostomes and many teleosts the two ovaries are issed. In many elasmobranchs the left ovary remains undeveloped; in birds and in the primitive mammall Ornithorhynchus the left alone matures. In amphibitions and reptiles the ovary is hollow, containing central lymph-filled cavities; in other cases the central part—the medula—is a connective tissue structure.

Testis. The early embryonic history of the testis, through the indifferent stage to the time of the development of primary sex cords (Fig. 281, C, p. 293) is similar to that of the ovary. From this point onward, the two diverge. No secondary sex cords are developed; it is the primary cords which produce a series of hollow structures in the walls of which the sperm mature. In anamniotes these structures are usually small spherical ampullae; in amniotes and some teleosts there are, instead, elongate seminiferous tubules (Fig. 286). They are lined by an epithelium in which are relatively rare supporting cells-Senoli cells-and the germinal elements. At the base of the epithelium are little-differentiated elements, the spermatogonia. From these are formed, after repeated divisions, the spermatozoa; when matured and released at the surface of the epithelium they include in their structure little except a head containing nuclear material and a long, mobile tail. Even in small animals the total production of these tiny gametes may be measured in billions. The ampullae in which sperm are produced in lower vertebrates are expendable, and are thus somewhat comparable to egg follicles. When sperm are discharged at a breeding season, the series of ampullae concerned are resorbed, to be replaced by others which have meanwhile developed



Fig. 286. A small area of a mammalian testis, showing one tubule and parts of several others in cross section and the intertubular tissue. (From Hooker in Fulton-Howell.)

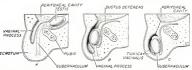


Fig. 287. Descent of the testis in mammals; ventral surface of body at left. A vaginal process develops from the body cavity; its peritoneum forms the vaginal tunic of the scrotal sac. Broken line in C. position of inguinal canal in mammals in which sac is not completely closed. (From Turner.)

more slowly. The seminiferous tubules of higher vertebrates, on the other hand, are characteristically permanent structures.

The testis tends to be, on the whole, a more compact and regularly shaped structure than the ovary, and does not undergo as marked seasonal changes. In cyclostomes the two testes fuse, and there may be a partial fusion in sharks; in various birds and mammals the left testis tends to be moderately larger than the right.

In most vertebrates the adult gonads retain a position in the upper part of the celonic cavity. In most mammals, however, there occurs a descent of the testis. Paired pouches, projecting externally as the scrotal sacs, form in the floor of the abdominal cavity. During development (Fig. 287) the testes move hackward and downward from their original position into these sacs, acach accompanied by its duct and by a fold of its proper mesentery—the gubernaculum. In some cases the sacs remain in open connection with the abdominal cavity, and the testes may be withdrawn into the body between breeding seasons. In other mammals the sacs may be permanently closed off, but there is, nevertheless, a weak spot here in the abdominal avail, rupture of which leads to the condition known in man as inguinal hernia. This unusual phenomenon of testicular descent appears to be associated with the fact that the internal temperatures of the mammal body are too high for the delicate process of sperm formation; the temperatures in the scrotal sacs are several degrees lower.

The Oriduct and Its Derivatires in Lower Vertebrates (Figs. 273, 274, pp. 285, 287). In cyclostome both eggs and sperm are shed into the celom and must find their own way to the posterior end of this cavity, where ca pair of pores afford them passage to the exterior. In all gnathostomes the sperm are conducted through closed tubes, but the eggs are still shed in most cases into the celom. They are not, however, really freed into this cavity for they are (except by accident) recreded through a funnel-like structure close beside the ovary, into a tube, the oxiduct. Along the course of the oviduct there may be formed specialized enlargements for various purposes: storage of eggs before laying, deposition of a shell, or retention of the egg during embryonic development and a subsequent "live" birth—the riziparous condition.\*

\* In contrast to the primitive osparous method, in which the egg is extruded and development takes place externally. Some distinguish from typical viviparity an ovoruparous method in which development is internal, but the young receive no nourishment from the mother.

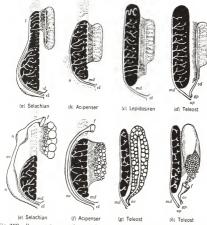


Fig. 28B. Representative types of urugenital systems in faiber. Upper series, males, lower series, femiles. Acipenter is a primitive actinopregrain. Lepladiume, the South American hangish. Black strain-harbot, vestigat in promptors, and the strain statistic strain processors and the strain state of the strain strain of the strain strain of the strain strain

The oviduat parallels the archinephric duct in its embryonic course, and in clasmobranchs and urodeles it is formed by a splitting in two of this duct. Possibly the female duct (like the typical male sperm duct) was originally derived from the urinary system but in most land vertebrates and in many fishes the oviduct forms independently, from mesodermal tissues, and thus shows no indication of such an origin. It is simple in structure in lungfishes and amphibians—forms which appear to be quite primitive in breeding habits. Beyond the proximal funnel, termed the infundibulum, the oviduet is a ciliated tube, small in diameter and relatively straight in resting phases; it may be expanded and highly convoluted at the breeding season. Its distal end may be especially enlarged as an orisac for egg storage. Oviduets of this primitive type may open individually into the cloaca, or the two tubes may fuse at their posterior ends.

In many teleosts, there is an exceptional situation in that countless thousands or even millions of eggs may be released during a short breeding season. Under the normal system of egg reception through an open funnel, it is obvious that there would be the danger, or rather the certainty, that the whole body cavity would be choked with eggs. In the teleosts this difficulty has been solved by sealing off, next to each ovary, a part of the celom into which the eggs are shed; from this the exit is into a funnel, not homologous to the true oviduct, leading to the exterior (Fig. 288, E. F.).

In sharklike fishes a large, shelled egg has evolved and a shell gland (nidamental gland) is formed as an expansion part-way down the oviduet. Here are present two types of glandular lining, one of which secretes an albuminous natical—"egg white"—about the egg; the other, in the lower part of the gland, forms a hard, horny egg case. Fertilization is internal in these cartilaginous fishes; the sperm travel "upstream" to fertilize the egg before it reaches the shell gland. Internal fertilization presumably developed because of the need for it in a form with a shelled egg. From this condition, however, it is easy to imagine the further step toward a viviparous condition, present in a considerable number of sharks and rays: the fertilized egg may be retained in the ovisac at the end of the duct until development is completed and the young born alive. In many elasmobranchs there is, still further, a development of methods of one sort or another whereby food materials may be furnished through the medium of the ovises lining as a contribution to the nourishment of the young in a fashion paralleling functionally the mammalian placents.

The Oxiduct in Anniotes—Uterus, Vagina (Figs. 274, B, 275, B, 287; 89, 287; 289). In amniotes, as in sharks, a shelled egg has brought about specializations of the oxiduct. In reptiles and birds the greater part of its length is the oxiduct proper, or uterine tube—muscular, broad and capable of great further distention at the breeding season. In anniotes, in contrast to sharks, the shell-forming gland is placed near the distal end of the tube, where the oxisac occurs in lower forms; it lies in the position of the utens of mammals and is frequently called by that name. Birds are universally oxiparous, but various lizards and snakes bear their young alive and in some cases have paralleled elasmobranchs and mammals in the development of structures through which nutriment may pass from mother to young. The two uteri of reptiles open separately into the cloacx; in birds the right oviduct, like the right ovary, is absent. In monotremes, which lay a shelled egg (although a relatively small one), the female organs are essentially similar to those of reptiles.

These organs, however, are markedly changed in typical mammals, in which the egg is tiny and development is viviparous. The uterine tube is a slender structure, The uterus, or womb, no longer produces a shell but is of the greatest importance as the place of development of the young. It is a thick-walled structure; is richly vascular epithelium forms, by union with the external membranes of the embryo, the placenta, through which maternal nourishment is afforded. In the most primitive mammals the two uteri are still quite separate, the duplex condition (Fig. 200); in most, however, the distal ends of the two are fused to give a

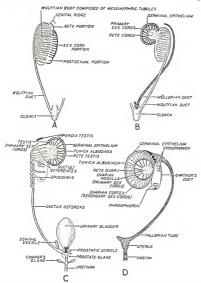


Fig. 289. Embryonic development of the genital system of amniotes. A, Early indifferent stage, showing sex cords, developing rete testis, mesonephric kidney and archinephric duct (wolffam body, wolffam duct), B, Somewhat later stage, in which the embryonic oviduct (millerian duct) has appeared. C, The adult male (cf. Fig. 282), D, Adult female (cf. Fig. 283), (From Turner.)

bipartite or bicornuate uterus; in higher primates there is complete union to a simplex type.

In reptiles and birds the most distal part of the oviducts, between uterus and cloaca, are short and undeveloped. In mammals, however, the terminal portions of the two dutes fuse to form a vagina for intromission of the male organ; the vagina opens into the urogenital sinus, derived from the cloaca. Marsupials show

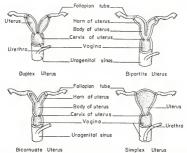


Fig. 290. Diagrams to show the progressive fusion of the posterior ends of the oviducts (fallopian tubes) in placental mammals. The uterus and part of the vagina have been cut open. (From Walker, after Wiedersteim)

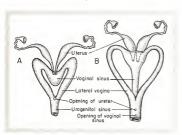


Fig. 291. Female genital organs of marsupials. A. Opossum; B. kangaroo. From a median vaginal sinus there develop, in the opossum, a pair of lateral vaginae which unite distally in the urinogenital sinus. In the kangaroo figured the vaginal sinus has developed into a median vaginal tube. (After Vandebroek.)

a curious (and surely aberrant) structure in which the vaginae are incompletely fused and may have a partly double—or even triple—construction (Fig. 291).

Sperm Transport: Epididymis, Ductus Deferens. In cyclostomes, we have have noted, the spermatozoa are discharged into the celorn and must make their own way to the outer world through pores at the back end of the abdomen. In all higher vertebrates this inefficient mode of transport has been abandoned and the male has developed a system of ejeculatory ducts which (in contrast with

the female duct system) is closed throughout its course. In most groups these ducts are clearly "borrowed" from the urinary system. As the testis develops it lies close beside the embryonic kidney (Fig. 279, p. 291). A short distance away are kidney tubules, from which the archinephric duct leads to the outer world. This short gap was bridged by the ancestral ganthostomes, and the sperm thus acquired a route to the exterior which could be followed in safety, avoiding the vicissitudes of travel through the eclonic wilderness.

Although there are variations of one sort or another, the connections between the seminiferous structures of the testis and the archinephric duct follow a basically similar pattern in most vertebrates (Fig. 292). Ripe ampullae or seminiferous tubules may be connected with one another by a central canal in the testis or a network of small canals, the rete testis. From this a number of parallel tubules extend across to the edge of the kidney. Here there may be a second longitudinal connection, or (as in mammals) the connecting tubules may pass discretally to a series of eststhich kidney tubules, which are termed ductall efferentes.

These tubules emerge into the archinephric duct, originally designed for urine transport. As we have noted in the earlier part of the chapter, a dual to be function, for conduction of both urine and semen, is functionally none too efficient and in the course of vertebrate history there has been a "struggle" between urinary and genital systems for use of the archinephric duct. As we have seen, the urinary system has tended to win out among bony fishes, and there has evolved a new duct for sperm transport. In most vertebrates, however, victory has gone to the genital system; the old archinephric duct has become a ductus deferens, serving for sperm transport alone.

The testis usually makes its connections with the anterior end of the kidney structure; as we have seen earlier in this chapter, urinary functions tend to be progressively concentrated posteriorly, and the front part of the old kidney system may become—most notably in mammals—a specialized region known as the epididymis. Even in sharks (Fig. 271, B) the anterior end of the archinephric duct may become highly convoluted as the ductus epididymis, and back of the actual region of testis connection with the duct there is a part of the original kidney modified into glands secreting a fluid which is believed to stimulate the sperm. In mammals (Figs. 282, p. 294; 289, C. 292, B) and in ammiotes generally the

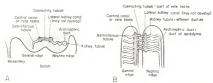


Fig. 292. A. Cross section of an anniote embryo, to illustrate the fact that testis and kidney are adpecent (cf. Fig. 279) and may thus readily come into counction by the development of bushes bridging the gas between sperm tubules and kidney bubbles. B. Digaramanic ventral two of a section of the and gential ridges to show mode of connection, usually with a central testis canal or rete testis between the sperm tubules with connecting tubules and frequently with a lateral kidney.

epididymis, containing the efferent ductules and convoluted duct, becomes a compact body resting close beside or upon the testis, as its name implies.

Distally the ductus deferens may expand into an ampulla for sperm storage in many groups, and in mammals (Figs. 282, p. 294; 289, C) there are further present other glands, including the prostate gland and seminal vesicles, which secrete liquid materials forming much of the seminal fluid.

## THE CLOACA AND ITS DERIVATIVES

In a great variety of vertebrates there is present at the back end of the trunk region a ventral pocket, opening to the exterior, in which are found the orifices of the digestive genital and urinary systems. This structure, appropriately termed the cloaca (the Roman name for a sewer), appears to have been a primitive vertebrate feature. We shall in this section follow, through the vertebrate groups, the history of the cloacal region and the varied disposition of the outlets of the systems concerned.

The Cloaca in Fishes and Lower Tetrapods. Embryologically the cloaca has a twofold origin (cf. Fig. 206,  $\Lambda$ , p. 230). Its major part consists of an expansion of the posterior end of the gut tube, which during much of development is closed off from the exterior by a membrane. External to the membrane lies a depression of the ectoderm, the protodoum. When the membrane disappears, this ectodermal area is incorporated into the cloaca, of which, however, it seems generally to form but a small part.

Among fishes, the cloaca is typically developed in elasmobranchs (Fig. 293, B). The major opening into it is that of the posterior end of the intestine; into it, further, open the urinary ducts and the sperm ducts of the male or the paired

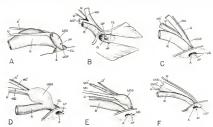


Fig. 293. Closed and and region in fabre. A. The lampers, Petromyzon, B., a fermule shark; C. a young fernale chinness: B. the Australian langish, Experientation, E. a female stargeon, F. a female share. Abbreviations: A amus. 4B\* abbosimial port; Gl. closex, G. graind opening. M. M.W. left and sharon. Abbreviations: A amus. 4B\* abbosimial port; Gl. closex, G. graind opening. M. M.W. left and right vinders of the lifter induceds; D(D), OFF, left and right vinders of the creal region of intesting. U. F. left and right urinary dacts; U.G. urinogenital opening; U.G.P. urinogenital popular, U.G. urinogenital space.

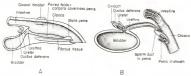


Fig. 294. Section of the closual regions of A. male tortoice, R. a monotreme mammal (Echidna). In A perimible structure is contained in the floor of the closus; paired folds may meet to form a take at the time of sperm emission. In the monotreme a formed year is present within the closus; it most hat, divided into several hazaches, for sperm transport, for the mice passes out via the closus. In most reptiles the ureter opens dorsally into the closus at a point for the properties of the closus of the closus. A surfar equeditation is not closured to the closus of the closus. A surfar equeditation is one. (4 purply of the closus of the closus. A surfar equeditation is one. (4 purply after Moreas, B after Keitel.)

oviduets of the female. The closea is likewise well developed in the lungfishes (Fig. 293. D) and in the sole surviving crossopterygian. In all other fish it is, however, reduced or absent. In hagfishes there is a shallow pocket representation as reduced closea, but in lampreys the urinary opening is separate. In lower ray-finned fishes and some teleosts urinary and reproductive tubes empty by a common sinus representing part of the closea, but the anus is distinct. In most televistal the systems have separate openings, and the same is true of chimaeras.

The primitive cloaca, however, was obviously present in the ancestral tetrapods, for it is found in all amphibians, reptiles and birds, with products of all three systems entering it (Figs. 273, 274, 275, pp. 286, 287, 294, A). Ventrally from the cloaca, we have noted, there develops in amphibians and many reptiles a large and distensible urinary bladder; this, however, generally has no direct connection with the ureters.

Fate of the Cloaca in Manmals. In manmals the lowly monotrenes (as the name indicates) still have a cloaca, but higher types have done away with this structure and have an anal opening separate from urinary and reproductive outlets. The monotreme cloaca (Fig. 294, B) shows a beginning of this subdivision. It is a unit for most of its extent, but the proximal part is subdivided into (1) a rectal region or coprodeum leading out from the intestine and (2) a more ventral undeam which cares for both urinary and genital products. In marsupials there is a shallow pocket representing a last vestige of the cloaca. In placental manmals this ancient structure has vanished. The coprodeum simply becomes the end portion of the gut, opening at the anus. The urodeum, however, has a more complex history and differs much in the two sexes.

Conditions here are best understood by considering the developmental story, which recapitulates rather well the phylogenetic history (Fig. 295). In a placental mammal there is at an early stage a closca formed by a distal expansion of the gut and separated by a membrane from the proctodeal depression. The architenphire ducts and the oviducts empty into a ventral part of the closca which extends outward to the allantois, and in which the bladder is to develop; the ure-ters presently develop and once here as well.

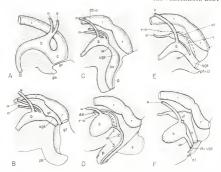


Fig. 295. Embryology of the closeal region of mammads diagrammate lateral views. A Sexually incidiferent stage, with intestine and allattosis opening into undivided closea, architephric dust and universe pointing together into base of allantois. R. Later indifferent stage, enaleyonic oxiders developed, unever opening together into base of allantois. R. Later indifferent stage, enaleyonic oxiders developed, unever and architephric dist becomes the dutto deferrors, game developed, unever the contract of male, and R. adult male structure. In contrast to female, the oxident disappears (levelose line in B), the architephric dust becomes the dutto deferrors, and an extensive urethra includes, in addition, (1) the base of the allantois, (2) the urgenital simus, and (3) a deut traversing the perior, E. Early stage of development of female, and F. adult female structure, disseparance of architephric dust (before the contraction of the cont

While the embryo is still in a sexually indifferent stage, a septum develops and extends outward to the closing membrane. This divides the closar into two chambers: a coprodeum, continuous with the gut above, and a urodeum, or ungenital sinus, below. Meanwhile, the bladder begins to expand, the ureters remaining in contact with it. Between bladder and urogenital sinus there is a relatively narrow if short tube which is to form part or all of the urethra of the adult; the sperm ducts and oviducts come to terminate at the point where this tube opens into the sinus (Fig. 295, B).

Beyond this stage, conditions in the two sexes diverge. In the female (Fig. 295, E, F) the urogenital sinus becomes the restibule of the urinary and genital systems; this may retain some depth (as in carnivores) or be a relatively shallow depression (as in primates). Into the vestibule open the conjoined distal ends of the oviducts as the vagina (the sperm ducts, of course, degenerate); into the vestibule also opens a relatively short urethral tube from the bladder.

In the male the sinus has a different history. It becomes an elongate tube which continues on into the penis. Into its proximal end open the sperm ducts (the oviducts degenerate) and the tube from the bladder. In the female this short proximal tube constitutes the entire urethra, but in the male the term urethra is applied to the whole extent of the tube from the bladder to the end of the penis. Female and male urethrae are, thus, not altogether comparable, for that of the male includes the homologues of both urethra and vestibule in the female.

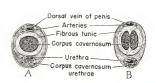
External Cenitalia. In primitive water-dwelling vertebrates with shellless eggs external fertilization is the general rule. But in forms with shelled eggs or with viviparous habits—including the Chondrichthyes, a few teleosts, and all amniotes—internal fertilization is a requirement, and special male structures are usually developed to facilitate the entrance of the sperm into the female genital tubes. In sharks, rays and chimaeras these take the form of claspers extending from the pectoral fins (Fig. 130, C, p. 160). These are inserted into the cloaca of the female; rolls of skin folded into tubes along the clasper form a channel for the sperm. In a number of viviparous teleosts a somewhat comparable median clasper is formed from the anal fin.

In ancestral anniotes direct contact of male and female cloacae would seem to have been sufficient for the transfer of sperm, for Sphenodon lacks copulatory organs, as do most birds. In many reptiles, however, the male has some type of accessory organ, a penis, to aid in sperm transfer. The hemipenes of snakes and lizards form a pair of cloacal pockets, often containing thorpilke spines; at the time of copulation these may be turned inside out, extruded, and inserted in the female cloaca.

In turtles and crocoditians there are structures which may be morphologic forerunners of the penis of mammals (Fig. 294, A). Lying in the ventral wall of the cloaca, with a groove between them, is a pair of longitudinal ridges, the corpora cavernosa penis, composed of spongy tissue (as the name implies); a further spongy structure, the glams penis, lies at the outer end of the groove. On excitation these structures are distended with blood and the glams inserted into the female cloaca; the groove between the cavernous bodies closes into a tube which carries the sperm. In the female a comparable but smaller structure is the cilioris.

In monotremes there are somewhat comparable structures, and the clitoris of the female manmal is in general relatively undeveloped. In higher mammals, however, the penis becomes a discrete external organ. Glans and corpora cavernosa are retained; the groove between the latter structures is closed to become the distal portion of the urethra and is surrounded by an additional cavernous body, the corpus cavernosum urethrae (Fig. 296).

Fig. 296. Sections through the penis of a rhesus monkey;  $A_*$  proximally, and  $B_*$  distally. (From Wislocki.)



# CIRCULATORY SYSTEM

In many small invertebrates there is no need for a circulatory system. Distances are short, and internal transportation of materials may be effected by diffusion and such flow of fluids as may result from body movement. With greater size and complexity, organization is required. A comparison with human communities is a fair analogy. In a village a transportation system is unnecessary; stores, school, church are all close to the homes they serve. With growth of the community this is no longer the case, and organized transportation systems are a necessity.

The simplest type of circulation seen among invertebrates is that of an open system, in which a heart forms a pump forcing blood out through a series of vessels-arteries-to various parts of the body. At the points where these vessels terminate, however, the blood is released into the tissue spaces to ooze back "on its own" to the heart. In Amphioxus an advance is seen in that return vessels to the heart-the veins-are present; in mid-course, however, the blood is still in contact with the body cells which it serves. Vertebrates have achieved a completely closed system in which, between arteries and veins, the blood is enclosed in a network of tiny vessels-the capillaries-and is never in direct contact with tissues. Higher vertebrates have, in addition, evolved a set of vessels, the lymphatics, which return blood from tissues to the heart,

Functions. Foremost of functions served by the blood is the active transport of materials to and from the cells (via the interstitial fluid). Oxygen must be constantly carried from gills, skin or lungs, and a small but steady stream of food materials-mainly glucose, fats and amino acids-must be supplied from the intestine or from storage and manufacturing centers, notably the liver. Conversely, wastes must be removed: carbon dioxide, destined for gills or lungs; nitrogenous wastes and excess metabolic water bound for the kidneys.

We have noted that maintenance of a stable and narrowly defined internal body environment is necessary for the welfare of the cells and tissues. The constant circulation of liquid throughout the body in the blood makes for uniformity of composition in the interstitial fluids of every region and aids in maintaining 308

relatively uniform temperatures. Among further functions of the circulatory system are aid in the struggle against disease and in the repair of injuries and, through the circulation of hormones, the utilization of the blood stream as an accessory nervous system.

### BLOOD

The blood, filling the vessels of the circulatory system, may be regarded as a tasse. Blood, like the connective and skeletal tissues, is derived from mesenchyme. Each of the three consists of cellular elements lying in a "matrix." In bone and cartilage the matrix is a solid substance; in connective tissue it is gelatinous in consistency; in blood the matrix is a liquid, in which the cellular components float in free fashion.

Blood Plasma. This liquid "matrix" of the blood, the plasma, is a watery fluid of complex composition. We have earlier noted the composition of the interstitial fluid surrounding the body cells, notably the complex and stable series of salts it contains in solution. The blood is essentially a part of this tissue series of salts it contains in solution. The blood is essentially a part of this tissue in contains the essentially a part of this tissue and the salts in addition, however, the blood contains materials peculiar to itself in the form of special blood proteins—allumin, globulins and fibrinogen, manufactured, it is believed, by the liver cells. These molecules are so large that they are normally unable to pass through capillary walls and thus leave the blood strone. The presence of the blood proteins raises the osmotic pressure of the blood above that of the interstitial fluids—a point of importance in capillary function. Further, the varied globulins play a variety of active roles, notably as antibodies effective against invading viruses, and the fibrinogen is the material which causes clot formation when a vessel is cru.

As well as these stable and permanent plasma constituents, the blood contains materials in transit—food materials, notably glucose, en route to the cells, nitrogenous wastes (mainly as urea or uric acid), carbon dioxide, and minute amounts of hormones.

Blood Cells (Fig. 297). Cellular blood components are absent in Amphioxus but are almost invariably present in vertebrates. They normally include (1) red blood corpuscles or erythrocytes, (2) white blood corpuscles or leukocytes, (3) thrombocytes.

Oxygen transportation is, on a percentage basis, the most important function of the circulatory system. Metallic compounds, particularly of iron or copper, are major aids in this regard and are found in many animals of various phyla, either free in the blood stream or contained in blood corpuscles. In the vertebrates the oxygen carrier is the iron compound hemoglobin; it is concentrated in the red blood corpuscles, the erythrocytes. In most vertebrates these are flattened oval structures which are proper nucleated cells. In mammals, however, the mature crythrocyte shed is in nucleus; further, in nearly all mammals (camels and llamas are exceptions) the corpuscles are circular rather than oval in outline. There is considerable variation in erythrocyte size; those of mammals may be but a few microns in diameter, but some amphibian corpuscles have a volume 100 times or more that of a typical mammalian corpuscles.

<sup>\*</sup> The term "serum" refers to the liquid remaining after the protein clot material (fibrin) has been removed from clotted plasma.



Fig. 297. Blood cells of A. a belose (Labray). B. a frog (Ram): C. a mammal (Labray). B. a frog (Ram): C. a mammal (C. hymbory). A. B. C. is outcopile gramlovytes. A. B. C. is outcopile gramlovytes. A. fine-grained axiolophile gramlovyte. A. fone-grained axiolophile gramlovyte. A. fone-grained axiolophile gramlovyte. A. S. fone-grained axiolophile gramlovyte. G. blood platelet. A. X. about 1200c. B. C. x. about 1200. (A soft 1200c. B. C. x. about 1200. (A soft Duthrie: B after Iordan; C after Maximos and Bloom.)

The white corpuscles, the leakocytes, are much fewer in number than the red corpuscles they constitute only about I per cent of the blood cells in typical anniotes but may rise as high as IO per cent in some fishes. Two main groups of white cells may be distinguished—lymphoid types, with a simple nucleus and clear cytoplasm, and granulocytes in which the nuclear materials are irregularly arranged and often subdivided and the cytoplasm is granular. Of the lymphoid leakocytes the common forms are the lymphocytes, small cells with a large nucleus and little cytoplasm. They derive their name from the fact that in mammals they abound in the lymph nodes; but they are equally abundant in lower groups where nodes are not present. To larger cells with a cytoplasm equally clear but more abundant, the term monocytes is applied.

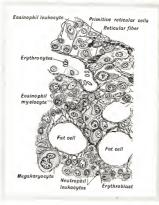
The granulacytes or polymorphonuclear leukocytes are large cells with a nucleus that is irregular or lobate and a cytoplasm that is abundant and highly granular. A type in which the granules stain readily with acid dyes is reasonably termed acidophilic (eosinophilic); others which stain with basic dyes or respond in part to both types of dye are, respectively, basophilic and heterophilic for neutrophilic). Heterophils of varied appearance are the most abundant granulocytes in all vertebrates (except reptiles), acidophils are widespread among vertebrate groups but rare in the individual; basophils are still fewer in numbers and are seldom reported in fishes. Despite much study, the functions of leukocytes are incompletely known; they accumulate rapidly, however, in injured or infected tissues where some appear to be phagocytes, "eating-cells," and others may aid in repair by transformation into connective issue elements.

Thrombocytes are blood elements associated with the process of blood clotting, In most vertebrate classes they take the form of small, oval, pointed spindle cells. In mammals there are present instead tiny blood platelets, which lack a nucleus. The disintegration of thrombocytes releases a material which functions in the chemical reactions needed to form the fibrin fibers which compose the blood clot

### BLOOD-FORMING TISSUES

In other body tissues, cellular differentiation commonly takes place in embryonic stages once and for all, and, furthermore, occurs in the place in which

Fig. 298. A blood-forming tissue—bone marrow from a nammalian femur. Much of the reticular framework and two reticular cells are seen, as well as two types of granular leukoytes in process of differentiation, and crythroblasts from which either of the properties o



the mature cells are found. Not so with the blood. The life of blood cells is measured in weeks or days, and these elements are constantly renewed. Further, the blood corpuscles are not fixed in position; once matured, they are free agents, which may circulate to any and every part of the body and carry with them no clue as to where or how they were formed. As a consequence, the study of the development and relationships of the blood cells is a difficult one, and there are many unsettled problems.

No part of the circulatory system is derived from any of the epithelial sheets laid down in the early embryo. In its entirety this system is derived, like the connective tissues, from the mesenchyme cells. Correlated, it would seem, with this embryonic relationship is the fact that in many instances cells of one of these systems appear to be transformable into members of the other.

Blood-forming tissues may be present in a number of areas in the body; these vary considerably from form to form and from embryonic sites to those present in the adult. In general, however, such sites have common structural features (Fig. 298). All are spaces which are enlargements of circulatory vessels or lie adjacent to such vessels. A reticular network of fibers forms the "skeleton" of the tissue. Emmeshed within this framework are found masses of blood cells in process of multiplication and differentiation. The seemingly simplest and elast differential type of cells found in such tissues are hemocytoblasts, a basic type of primitive blood cell from which either red or white corpuscles may develop.

Blood-Forming Sites. The first blood vessels formed in the embryo are

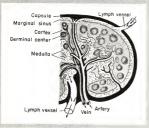


Fig. 299. Diagram of the structure of a lymph nodule. In addition to the lymph vessels, a nodule is supplied by a small artery and vein. (After Portmann, Einführung in die vergleichende Morphologie der Wirbeltiere, Benno Schwabe & Co.)

those engaged in bringing food materials, and the first blood cells are erythrocytes formed in connection with them. These early cells are, in consequence, formed in mesenchyme in the yolk-filled belly floor in forms with a mesolecule egg type, and in clusters of similar cells, termed blood islands (Fig. 248, A, p. 201), on the surface of the yolk sac in large-yolked eggs. At a somewhat later stage blood cells may arise in a variety of regions from the mesenchyme or from the walls of blood vessels. Favored areas in the embryo include the kidney, liver, spleen, and throat tissues, particularly the thymus.

Even in the adult a great variety of organs may contain blood-forming centers in one group or another. In lampreys, many teleosts and amphibians, the kidney continues to be important throughout life for blood cell production, and in these forms and in turtles the liver contains blood-forming tissue. In sharks white cells are formed in the gonds. Lymphodi tissues continue to be present in the throat in various forms, from fish to mammals, as tonsil-like cell masses. In higher vertebrates the bome marrow is a great center of blood formation; in this way the bollow interiors of long bones are put to positive use. In some frogs and in reptiles and birds all types of blood cells are produced in the marrow. In mammals, however, there appears to be no release of lymphocytes into the blood stream from the bone marrow. This cell type, instead, is found to be stored and multiplied in the lymph nodes (Fig. 299), small spherical organs situated along the course of lymph vessels. A few lymph nodes may be found in birds, but no such structures are present in lower vertebrate classes.

Spleen. Only in the case of the spleen do we find tissues associated with blood-cell formation or storage assuming the condition of a discrete major organ. In cyclostomes even the spleen is present merely as a mass of reticular blood-tissue surrounding part of the gut. But in every other vertebrate group it is, although adjacent to the gut, a distinct reddish structure lying in the dorsal mesentery. As may be seen from Figure 300, it may attain a complex structure. Within its reticular framework are packed masses of blood cells which in localized areas form either a white pulp consisting of leukocytes or a red pulp in which red cells predominate. The spleen is fed by an artery and drained by a vein, both of which may branch in complicated fashion; no lymphatic vessels are present.

CIRCULATORY SYSTEM 313

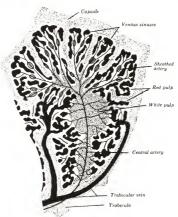


Fig. 300. Diagram of a part of the mammalian spleen. Venous spaces in black; white pulp, heavy stipple: connective tissue capsule and trabeculae, light stipple: red pulp, unstippled. "Sheathed arteries" are surrounded by white pulp. (From Finnerty and Cowdry.)

The spleen is in every group an important center of blood cell formation. In the embryo, crythrocytes as well as leukocytes are formed there, and this function persists in the adult except in mammals, where bone marrow has become the important seat of crythrocyte formation and white cells alone mature in the spleen. Red cells are, however, stored in great quantities in the spleen, in mammals as in lower groups, and destruction of such cells occurs here as well, to at least some degree.

## CIRCULATORY VESSELS

The vessels of the circulatory system, like the blood cells, are derived from the body of the early embryonic mesenchyme. As food-containing liquid begins to flow through the body of the early embryo, adjacent mesenchyme cells gather about such channels and surround them with a continuous wall. All early formation of vessels takes place in this fashion; later in development and in adult life, new vessels may form (as tissues expand or injuries are repaired) by outgrowths from the lining

of channels already established. The inner lining of blood vessels, termed an endothelium, consists of thin, leaf-shaped cells, continuous with one another at their margins. Nowhere is the circulating fluid in direct contact with the interestitial fluid or body cells, although most of the plasma contents can pass freely through the thin endothelial membrane.

The vessels of the circulatory system include (1) the heart; (2) arteries, by definition vessels carrying blood from heart to body tissues; (3) capillaries and comparable structures, typically very small vessels connecting arteries and veins; (4) veins, returning blood to or toward the heart; and (5) lymphatics, auxiliary vessels prominent in higher vertebrates, which aid in the return of fluid from the tissues.

Capillaries (Figs. 301, 302). These smallest of vessels, whose walls consist solely of a thin endohelial layer, generally have only the "bore" necessary to allow an crythrocyte to pass; they typically deploy from the ends of the arterial branches, wind among the tissues in such fashion that no cell is far from a capillary, and at their distal ends are re-collected into veins. Capillary networks, however, may be interpolated along the course of arterial for venous systems. In gill-bearing vertebrates the course of arterial flow from the heart is interrupted by a capillary system in the gills. The return of venous blood from tissues to heart may be interrupted also by a forced passage, on the way, through a network of capillaries or similar vessels, as happens in the liver in all vertebrates and in the kidneys in many groups. An interjected system of veins which lead the blood to

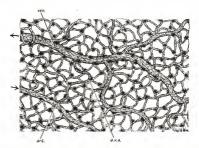


Fig. 301. Portion of a capillary bed from the web of a frog's foot, showing small arteriole (art.) and venule (ern.), a capillary network, and a direct arterio-venous anastomosis (a.v.a.). (From Young, The Life of Mammals, Oxford University Press.)

<sup>\*</sup> We are accustomed to think, in visual images, of arterial blood as oxygenated and hence "red"; but atterial blood between heart and gills in a fish, is, of course, of the "blue" wonous type; the arteries and veins leading to and from the tetrapod lung likewise have a reversal of the "blue" and "red" blood types.



a capillary "portal" in some organ rather than returning directly to the heart is termed a portal system.

Although capillaries are the major intermediaries between arteries and veins, there are other types of connections. There are sometimes found direct "short circuits" of larger caliber-anastomoses-between arteries and veins, or there may be substituted for capillaries small, thin-walled "ponds" of blood termed sinusoids.

Capillaries are too small to be dissected by ordinary means and hence are neglected from the point of view of gross anatomy. But it must never be forgotten that functionally the capillaries are the most important part of the circulatory system. Elsewhere blood is merely in transit; here it is at work, exchanging with the interstitial fluid, and through this with the cells, oxygen and food materials for carbon dioxide and wastes. At the proximal end of a capillary system the balance between hydrostatic pressure, tending to force materials out of the capillaries, and osmotic pressure is such that oxygen and other materials in solution pass out of the blood and to the tissues; at the far ends of the capillaries, hydrostatic pressure is, of course, lessened, and osmotic differences between blood and external fluid favor an inflow of carbon dioxide and wastes.

Arteries and Veins (Figs, 303, 304). The larger vessels of the body, arteries and veins, their smaller branches, the arterioles and venules, and likewise the major lymphatic vessels have external sheathing materials in their walls in addition to the ubiquitous endothelium. These include connective tissue fibers, clastic fibers and smooth muscle cells in variable amounts; in the walls of large arteries or veins there may be small nutrient blood vessels for these tissues. The walls of the large vessels are customarily described as consisting of three layers of "tunics," the tunica intima, tunica media, and tunica externa or adventitia. As seen in small vessels the intima may consist only of the endothelium, but in a large artery there may be here also a thin sheet of connective tissue and a sheath of elastic tissue, the internal elastic membrane. The tunica media is dominantly a sheath of smooth muscle, which in large vessels is generally arranged in two lay-

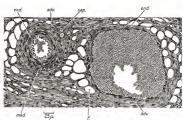


Fig. 303. Section through a small artery and its accompanying vein, showing contrast in size and thickness of walls. adv., Adventitis; cap., capillary; end., endothelium; f, fat cell; med., media (muscle layer) of after, (From Young, after Maximow and Bloom).

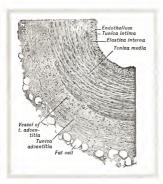


Fig. 304. Section through an artery of a mammal. (After Schaffer.)

ers, of circular and longitudinal fibers. Sometimes the tunica media is bounded externally by a second elastic membrane. Beyond this is the adventitia—connective tissue, often rather loose, which binds the vessel to adjacent structures. Arteries and veins have a somewhat similar build, but the veins (as may be seen in Figure 303) are typically thinner-walled and of larger caliber than comparable arteries. These differences are, of course, obviously related to the fact that arterial blood is flowing under higher pressure and at higher speed than that of the veins.

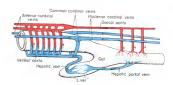
These functional differences account for further contrasts between arteries and veins. The "bore" of an artery tends to remain constant, diminishing only as branches are given off, a vein may expand along its course to form a large sac or sinus. The arterial system presents few individual anomalies, but veins are or sinus. The arterial system presents few individual anomalies, but veins are highly variable. A fast-flowing mountain stream tends to take a direct and undeviating course, whereas a sluggish stream meanders, branches and re-forms, produces islands; so in the embryo a vein offen appears as a network of variable channels (cf. Fig. 329, p. 338); which channels are to form the definitive vein are not fixed, and hence the frequent anomalies. In veins there are often developed radres, commonly in pairs. These are folds of the intima, behind which lie pocket-like depressions. A backward flow of liquid in a sluggish vein is prevented by distention of the pockets and a consequent closing of the vessels. Almost never are such structures present in an artery, since arterial blood cannot ordinarily work back against the heart valves.

#### ARTERIAL SYSTEM

Aortic Arch System in Fishes (Figs. 305, 306, 309). In primitive, gill-breathing vertebrates (and in Amphioxus as well) all the blood from the heart courses forward in a ventral aorta lying in the floor of the throat. From this a series of nortic archess' curve upward on either side between successive gill slits. Each breaks up into capillaries on the gill membranes for aeration of the blood and is reformed dorsally into further arterial vessels which pass to the tissues of the body and head. In land vertebrates the gills are lost, but arch vessels are found in every embryo. The history of the aortic arches is one of the most interesting chapters in the structural evolution of the vertebrates.

In a diagrammatic primitive vertebrate (Fig. 309, A) we may picture the aortic circulation as including paired arches passing upward laterally in front of or between each gill slit or pouch and, beyond the capillary network, reaching

Fig. 305. Diagram of the major circulatory vessels of Amphitosa. Except for the absence of a heart as the posterior end of the ventral aorta, the system is closely comparable to that of vertebrates. Only a few of the numerous aortic arches are shown. Capillar systems are not shown except those concerned with the hepatic portal system. (The vessels are colored as if oxygen intake were entirely through gill walls, which is, of course, not the case.)



<sup>\*</sup> The triple use of the word "arch" in the gill region was commented on earlier; in this chapter acrtic arch is implied throughout.

the dorsal aorta. Posteriorly this major vessel is a single median trunk carrying blood backward to body organs, anteriorly it consists of a pair of vessels, one on either side of the head. The number of aortic arches was presumably high and variable in the ancestral vertebrates (it is very high in Amphioxus), part from cyclostomes and a very few sharks, however, there are normally in vertebrates but five gill slits plus a spiracle and hence potentially six aortic arches, usually designated by Roman numerals. In vertebrate embryos these arches develop, in general, in regular order from front to back, and until the gills begin to function the arches in fishes are continuous, uninterrupted vessels.

Vertebrates invariably refuse to adapt themselves to a man-made structural diagram, however, and in the aortic arches, as elsewhere, the "idealized" condition we have pictured is never preserved in the adult. There is considerable variation in the afferent and efferent portions of the arch when the gill capillaries develop in fishes, Diagrammatically, we have represented the arches as distributed so that one supplies each gill (i.e., each gill bar); but in lampreys the arrangement is such that each arch supplies both front and back portions of a gill pouch, and in sharks the efferents are similarly placed opposite each gill slit. The maner in which an arch "breaks up" into eaplilary systems results in differents in the arrangement of afferent and efferent vessels, variations in different fish groups in this regard are shown in Figure 310. Other variations of a confusing sort lie in the presence of small efferent vessels (not shown in our figures) which may supply the tissues of the throat region or the heart.

Most striking is the fact that in jawed fishes, in which six arches always devolop in the embryo, certain of them are invariably lost or modified. This is the case with the mandibular arch. In living gnathostomes it frequently appears prominently in the embryo but never persists, except for its dorsal portion, which may aid in the blood supply to the head (Fig. 306, spiracular artery; cf. Fig. 309, B). The second aortic arch—the byoidean—is well developed in the Chondrichthyes, but this too is lost in most ray-finned fishes and the lungfish Epiceratodus. Still another variant is that in the African lungfish Protopterus, which depends largely on lungs for breathing purposes, where arches III and IV run without break past

the gill region.

"Aortic Arches in Amphibians (Figs. 309, £, 311, 4). In the amphibian stage further changes occur in the arches, but in great measure the adult structure is not too far from that seen in the more advanced fishes—barring the fact that the vessels, with loss of gill breathing, are continuous tubes. In the frog larva, gill capillaries are developed only to disappear later, but in urodeles, in which internal gills never develope, the arches remain as uninterrupted structures from embryo directly to adult. As in the more progressive fishes the first and second arches disappear during embryonic life. In many urodeles all the remaining four arches may persist, but arch V is absent in some urodeles and all anurans, leaving III, IV and VI as the persistent members of the series.

Changes, however, occur in the dorsal connections of the arches. Even in fishes, blood flowing upward in arch III tends to pass forward toward the head rather than back toward the body, in tetrapods this arch and the continuation of the dorsal aorta forward from it become the internal carotid artery. A vessel runing forward ventrally toward the tongue region from the back of the third arch develops as a lingual artery, and the end of the ventral aorta leading to both vessels is the common carotid. Back of the carotid, the segment of the dorsal aorta connecting it with the succeeding arches disappears in some amphibians and is

absent in the great majority of amniotes; where it persists it is termed the carotid duct.

Arch IV is always a large paired vessel in lower tetrapods; it is termed the systemic arch, since it is the main channel for blood flowing from heart to body. Why this arch was selected as the channel, rather than the shorter and more direct route via arch V, is an unsolved puzzle.

The lung in tetrapods receives its blood from a pulmonary artery leading back from arch VI. During the larval life of an amphibian, when the lung does not function, most of the blood in this arch travels straight up into the dorsal aorta as part of the main blood stream to the body. When air breathing begins, the blood stream in this arch is diverted to the lung. The dorsal part of the arch, now unimportant, disappears in frogs and most ammiotes; it persists, however, in reduced form among urodeles, the Apoda and a few reptiles, where it is called the ducus arteriosus. The base of the ventral aorta tends to divide, with separation from the main vessel of a pulmonary trunk.

In sum, we see in amphibians a strong trend toward separation of the old arch system into three parts: (1) a pair of carotids supplying the head region; (2) a pair of systemic arches supplying the body, and (3) a pair of pulmonary arteries to the lungs, which arise from the heart by a trunk separate from that leading to the other two croups.

Amniote Aorite Arches. Further specialization of the arch system in the amniotes has to do mainly with the systemic arch, in which asymmetry replaces the originally symmetrically paired conditions. In amphibians, as we have seen, both systemic arches, and the carotida as well, leave the heart through a common trunk. In living replies there are, instead, two trunks (Fig. 311, C, D), One—the smaller of the two—leads only to the left systemic arch. The other and much larger vessel supplies both carotids and a right systemic arch which is larger than its mate. The base of the two openings from the heart are so situated that the larger opening receives "fresh" blood from the lungs, whereas the left arch mainly recirculates "senous" blood back to the body and has little function (except that of relieving the lungs of too great a volume of blood). In birds (Fig. 309, C) this vessel disappears, and head and body are served by a single great anota which follows the path of the right fourth sortic arch.

Mammalian arch evolution has followed a different path. Mammal ancestors diverged from those of modern replifies at a very early stage, and there is no reason to believe that the split between the vessels leading to the two systemic arches ever occurred. But even so, a double arch is unnecessary and inefficient; somewhere along the line leading to mammals the fourth right arch disappeared from the picture. The mammal, like the bird, has simplified the systemic blood supply; but whereas the birds have held to the right arch, in mammals it is the left member of the pair that has become the great arch of the aort.

In mammals both carotids and both arteries to the pectoral limbs (the subclavians) are supplied with blood from this same great trunk. There are, however, great variations in their mode of branching, some of which are shown in Figure 312.

The embryonic development of the aortic arches of a mammal recapitulates to a considerable degree the phylogenetic story outlined above (Fig. 313). The first blood channel from heart to body is that of arch I. Gill pouches develop back of this arch, and successive aortic loops—II, III, and IV—are formed between them; arch V appears as a transitory structure in some instances, and finally

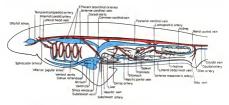


Fig. 306. Diagram of the main blood vessels of a shark as seen in lateral view.

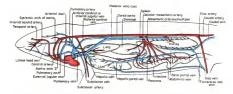


Fig. 307. Diagram of the main blood vessels of a urodele amphibian as seen in lateral view.

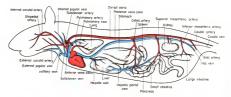


Fig. 308. Diagram of the main blood vessels of a mammal (rat) as seen in lateral view.

CIRCULATORY SYSTEM 321

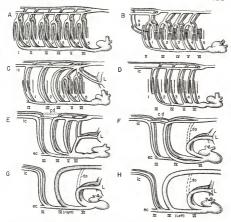


Fig. 309. Diagrams of the aortic arches and derived vessels in various vertebrate types. A. Theoretic cal ancestor of the yaved vertebrates with its unspecialized notice arches, B., typical fish condition as seen in a shark; C. the langish Protopterus, D. a teleost; E. a terrestrial salamander, F. a lirand; G. a binti; H. a namual. Various accessory cessels are omitted. The vessels of the right side architecture with a shark of the right side architecture and the propose of the diagram to correspond more or less to that of the arches from which they are derived. Aortic arches in Roman numerals, s. spiracular slit; following fill slits in Arabic numerals, cd. Carodid duct; ds, embryonic dactus arterious, except and the processor of the carolida strets, is citerial carodid artery, L. lang. The carolida duct shown in the lizard is absent in other reptiles; in turtles the carolida strise by a separate stem directly from the heart. In H the embryonic arterial duct by possing the lungs is shown in bedeen lines.

arch VI develops. As the more posterior arches form, the more anterior ones become reduced in importance; I and II disappear, and III becomes distinct as the carotid. The blood in arch VI in the embryo passes upward to the dorsal aorta and little of it enters the pulmonary artery until birth, at which time the upper part of this arch—the arterial duct—is occluded. Meanwhile the pulmonary trunk has separated from the aorta, the right fourth arch has disappeared, and the carotid duct has closed. The mammalian embryo thus reviews for us the evolutionary history of the aortic arches.

Blood Supply to the Head (Fig. 314). In fishes the cranial region is

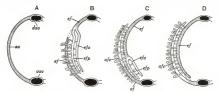


Fig. 310. Diagram of circulation in a fish gill, left side, from behind. A, Embryonic condition, with continuous aortic arch, on, from ventral aorta, row, to donal aorta, don B, Shark condition; the affecting gill vessel, of, is formed from the aortic arch; the paired efferent vessels, de, δp, are new formation. C, Condition transitional to D, seen in sturgoous. D, Teleost condition. The embryonic arch gives to the effective vessel, off; the affective vessel, dp, is a new formation, (After Seventrali, Cooldrie).

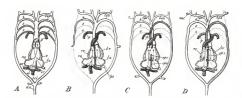


Fig. 311. Diagram of the heart and aortic arches in tetrapods. A, Amphibian; B, a mammal; C, typical modern reptiles; D. crocodilian. Ventral views; the heart (sectioned) is represented as if the chamhers were arranged in the same plane; the dorsal ends of the arches are arbitrarily placed at either side. Solid arrows represent the main stream of venous blood; arrows with broken line the blood coming from the lung. Vessels with aerated blood are unshaded; those leaving heart with venous blood, hatched. The two vessels at the top of each figure are the internal carotid (laterally) and external carotid (medially). In amphibians without a ventricular septum the two blood streams are somewhat mixed; subdivision of the arterial cone tends to bring about partial separation, but some venous blood is returned to the dorsal aorta. In mammals ventricular separation is complete, the arterial cone subdivided into two vessels, and the arches are reduced to the left systemic and pulmonary. The mammalian condition has apparently arisen directly from the primitive type preserved in the Amphibia, for in modern reptiles the conus arteriosus shows a division into three vessels, rather than two; one, returning venous blood back to the body, leads only to the left fourth arch. In crocodilians the ventricular septum is nearly complete, and the elimination of the left fourth arch would give the avian condition. asc, Anterior subclavian; d, duetus Botalli; da, dorsal aorta; la, left atrium; lsa, left systemic arch; lv, left ventricle; p, pulmonary artery; pv, pulmonary vein; r, portion of lateral aorta remaining open in some reptiles; ra, right atrium; rsa, right systemic arch; rv, right ventricle; spa, interatrial septum; spv, interventricular septum; sr. sinus venosus; v, ventricle; vc, anterior vena cava; vcz, posterior vena cava. (From Goodrich.)

CIRCULATORY SYSTEM 323

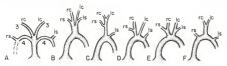


Fig. 312. Diagrams, in vertral view, to show variations in the branching of the main blood vested from the nammalian nortic arch. A, Embysuic conditions, with vestral transk of acut and third contribution of the substitution of the substitution of the substitution of the substitution by differential growth of the vested the various arrangements shown in B to brought about (D is the human type),  $k_c$  Left carotic,  $k_c$  left subclavian;  $m_c$  right carotic,  $m_c$ 

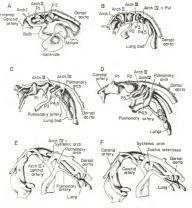


Fig. 313. Development of the nortic arches of a mammal (Homo). The outline of the gat cavity, gill possebes, and lung holds are shown in addition to blood vessels; in A, the cavities within the heart are included. Arch I is developed, B, Arch I already reduced, II and III formed, C, Arch II reduced, N/ (systemic) formed, VI (pulmonary) arch and pulmonary artery forming (Arch V does not develop in man). D, Pulmonary arch well developed, E, Carotid arch (III) persparted deveally from noste, pulmonary the becoming distinct at root from ventral aseta. F, Dagrant so show reduction at birth of upper end of arch VI (ductua arteriosa). P¹ to P² = parageal powhers, Alfor Sixvetery.

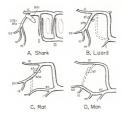


Fig. 314. Diagrams of the left side of the bead to show the evolution of the caucid system. In a relatively primitive fish stage (4) the direct forward continuation of the acut is the internal cancidal attery, which enters the braincase near the pituitary. This gives of a major branch, the orbital attery, which such that the beautiful properties of the work of the size of the stage of the properties of the stage of the passes close to or through the stapes (= hyomandibular). However, a small branch present near the passes close to or through the stapes (= hyomandibular). However, a small branch present near the toro of the carotide extends forward, and as the external carotid of manumals may take over part of all (B) of the functions of the stapedul, ee, External carotid, fan, hyomandibular, ic, internal carotid; in, infraorbital attery, I, fingual artery, e., mandibular attery, evo, obtain attery, so, suprarchital attery, ill, Ill, second and third nortic arches. In B to D modified nortic root = common carotid.

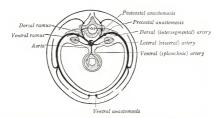


Fig. 31.5. Diagrammatic cross section of the body of a higher vertebrate to show various types of branches which may be given off by the aorta. Most prominent are median ventral branches descending in the mesentery to the gut, and so forth, and paired interregeneral arteries, the main ventral ramus of which descends the flanks between the myomeres or adjacent to successive risk. Longitudinal anastomoses may occur between successive segments in various persions. (From Arca Persion Section 1997).

supplied with arterial blood by the paired vessels which form the anterior end of the dorsal aorta, running forward along either side of the head, as we have seen, this becomes in land vertebrates the internal carotid artery. The main trunk of this artery passes upward into the braincase in front of the pituitary. Before doing this, however, it gives of a major branch, an orbital artery, to supply much of the face and jaw region. This same situation holds true in most groups of land vertebrates, including some mammals, where the homologue of the orbital artery is the stupedial artery, so named because it often passes through an opening in this auditory ossicle.

We have, however, noted that in early land vertebrates a small lingual artery series thich supplied blood to the tongue region. In mammals generally this becomes enlarged and elongated as the external carotid artery. It takes over the supply to the lower jaws, frequently that to the upper jaws, and in many forms (as in man) even supplies blood to the face, so that the stapedial artery is lost. The process is analogous to that of "stream prizey," whereby one river system

taps the headwaters of another.

Blood Supply to the Body and Limbs (Figs. 306-308, p. 320; 315). In every vertebrate the major blood supply to the trunk, tail and limbs is furnished by the dorsal aorta. Although paired anteriorly, the aorta in the trunk is a single median vessel, lying beneath the backbone and above the root of the mesentery. Two types of branches develop: median ventral ones running down the mesenteries to the gut and its derivatives (liver and pancreas), and paired lateral branches, mainly to the muscles, skin and other tissues of the body walls. The ventral-"splanchnic"-vessels are numerous in the embryo, but in adults are usually concentrated into a few main trunks, including a celiac artery to the stomach and liver and one or more mesenteric arteries to the intestine. Short lateral branches from the aorta reach the kidneys and gonads. Longer branches to the "outer tube" of the body were primitively segmental and remain essentially in that condition in many lower vertebrates. In more advanced groups, however, we find that longitudinal connecting channels may form anastomoses at several points, both dorsally and ventrally. As a result there is a trend for reduction in the number of arteries coming from the aorta, leaving a relatively few large arteries, each of which may serve a considerable area of the back and flank.

In embryonic development a paired fin or leg is supplied by a network of small arteries (Fig. 329, p. 338). During ontogeny one or another of these tends to become dominant and form a main channel from aorta to limb. In the pectoral appendage the main trunk is usually given its mammalian name of subclavian artery as it enters the limb; various other terms (as axillary and brachial) are applied to this same main vessel as it progresses distally. In the pelvic appendage the primitive trunk was the ischiadic artery, which emerged back of the pelvic girdle; in mammals, however, the major stem is the femoral artery, running out to the limb in front of the ilium (it is termed popliteal and peroneal father distalls).

# VENOUS SYSTEM

The veins—vessels bringing blood from capillary systems toward the heart have a complicated and variable arrangement. If, however, their embryonic history is studied, it is seen that they can be logically sorted out into a small number of systems. From this point of view we can distinguish (Fig. 316):

 A subintestinal system flowing forward beneath the gut in the embryo, and in the adult divided into the hepatic portal system running to the liver and the hepatic veries from liver toward the heart.

- Veins situated dorsal to the celom or gut and carrying blood toward the heart from the dorsal part of the body and the head (and generally from the paired limbs as well); they include the cardinals or the venae carae which replace them, and their affluents.
- A relatively minor group, the abdominal vein or veins, draining the ventral part of the body wall in most classes.
  - 4. In lung-bearing forms, the pulmonary veins from lung to heart.

The first and fourth of these four components form the drainage of the gut tube and its outgrowths; it is essentially a visceral venous system. The second and third components are, on the contrary, mainly somatic venous elements, draining the outer wall of the body.

Hepatic Portal System and Hepatic Veins (Figs. 306–308, p. 320). The hepatic portal system, common to all vertebrates, is composed of veins which collect blood from the intestine and transport it to the sinusoids of the liver. It is functionally of the highest importance, since its presence guarantees that the liver had "first chance," for storage or transformation, at food materials absorbed by the intestinal capillaries.

Beyond the liver sinusoids the blood from the intestine is re-collected into a hepatic rein or veins. In most fishes this is a large vessel which empties directly into the heart. In sarcopterygian fishes and tetrapods, however, we find that, as discussed later (p. 330), part of the hepatic vein system has been incorporated in the posterior vena cava. In consequence, the term "hepatic vein" is restricted in these forms to the vessel or its subdivisions which empty from the liver into the terminal part of the vena cava.

Generally the first blood vessels to appear in the embryo in forms with a mesolecithal type of egg are a pair of veins which form in the floor of the gut and coalesce into a single channel running forward ventrally as a subintestinal vein (Fig. 330, p. 338). From the far anterior end of this trunk develop the heart and the ventral aorta—structures with which we are not concerned at this point. The remainder of this vessel gives rise to the hepatic and hepatic portal veins. For a time this runs without break from intestine to heart. Presently, however, the liver grows out ventrally from the gut. With its growth, liver and vein mate-

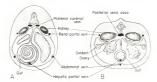


Fig. 316. A, Cross section of the abdominal region of a shark, to show the position of the main veins B, The same in a urodele amphibian.

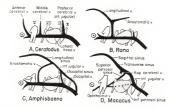


Fig. 317. Diagrams of the left side of the head region to abov stages in the evolution of the venous drainage. Rost of some of razial networs are indicated, the position of the eye is shown, and the oile capacitie is stippled. In lower vertebrates the main drainage is by a law blood venic, which forms in the orbital region and runs backward to become the anterior exceed and. This printingly receives several too. creative venic from the interior of the Sull. A series of sinuses developed in the brainsness the lateral head vein is shandoned in mammals, and blood from the orbital region on this upstant of the head vein is shandoned in mammals, and blood from the orbital region on the sum system, at fit, and the contraction of the sum of the

rials become intermingled; the vein breaks up into small vessels and finally into a liver sinusoid system, with the resulting formation of a separate portal trunk posteriorly and a hepatic vein anteriorly (Fig. 332, p. 339). In large-yolked types a basically similar process of vein formation occurs, except that, as described in a later section, vitelline veins replace the subintestinal vessel in gathering food material from the yolk sac. In typical fishes no further important development occurs; in the embryo of lungfishes and of higher vertebrates a branch of the hepatic vein reaches dorsally along the mesenteries to tap the posterior cardinal system and form the anterior part of the posterior vena cava (p. 330). The hepatic portal vein remains a large and important vessel collecting blood not play from the intestine, but from the stomach, pancreas and spleen as well, for conduction forward to the liver.

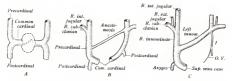


Fig. 318. Ventral views of the veins anterior to the heart region in successive developmental stages to show the formation, in man and certain other manmals, of a single anterior (or superior) vena cava from the two anterior cardinals (precardinals). An interconstal vieit [f) and a small voin from the wall of the left artism  $(0.F_{\nu}$ , oblique vein) are perisating vestiges of the original left anterior cardinal. (From Arcy.)

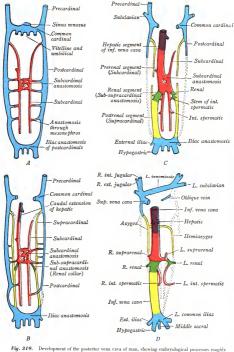


Fig. 319. Development of the posterior vena cava of man, showing embryological processes mughly paralleling the evolutionary history. The original posterialis system is show in blue. Presently there develop subcardinal vessels, corresponding to the veins draining the kidney when a portal system is esultablished in sharts. In B, this venous system is tapped is in langifished ye harmed of the fusive veins (purple). A third system of embryonic veins, the supracardinals (yellow) is not exactly paralleled in phylogows. In genera new seasis which develop in a manifest so bipass the kidney and eliminate he read portal system. As seen in D, the definitive posterior vena cava includes fractions of all those structures; (From Area, Agir McClure and Buffer)

Dorsal Veins—Cardinals and Venae Carae. The principal blood drainage from the "outer tube" of the body is cared for by important longitudinal vessels situated dorsally above the gut and mesenteries. In lower vertebrates these veins are the cardinals; in higher forms major modifications of these vessels produce the venae cavae.

In the embryo of every vertebrate (and of Amphioxus as well) paired veins appear at an early stage in the tissues above the celomic cavity, one on either side of the midline (Fig. 331). These are the primitive cardinal reins. The posterior cardinals run forward along the trunk on either side of the dorsal norta to the heart. Paired anierior cardinals begin as head veins on either side of the developing braincase and run back dorsally on either side of the neck region to meet their posterior mates. From their point of junction on either side a major vessel descends to enter the sinus venosus of the heart; this is the common cardinal (or duct of Cuvier). This characteristic cardinal system is retained in the adult of most fishes (Fig. 306, p. 320). We may discuss separately the history of its anterior and posterior parts.

In all vertebrates except mammals the main stem of each anterior cardinal begins as a lateral head vein (Fig. 317, A–C) arising behind the orbit, receiving tributaries from face and brain; traveling back past the ear region to the level of the occiput, they are then termed anterior cardinals, and continue in typical fishes back to the common cardinals, receiving the veins from the pectoral appendages on the way. In lungfishes and tetrapods the posterior cardinals (as we shall see) are so modified and reduced that the common cardinals are merely continuations of the anterior trunks. With this modification the anterior cardinals come to resemble the vessels termed anterior venac cavae in mammals and are frequently called by this name.

(Fig. 317, D). A sinus system is established within the expanded brain cavity, Blood from much of the front part of the head enters the braincase to emerge posteriorly as the internal jugular reins and then, joining more superficial vesels, the external jugulars, to form common jugulars; the old lateral head vein is lost. After a junction with the vein from the front limb the vessel is termed in mammals an enterior vena cave. Despite the change in name, however, it is easily

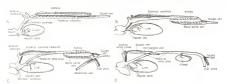


Fig. 320. Diagrams in lateral view to show the evolution of the posterior cardinals and the development of a posterior vena cava. A Lampecy (larva); B, typical fish condition; interjection of renal portal system. C, Lamgish or primitive tetrapod; a shortened route to the heart is established by utilizing part of the hepsits vein system in the initiation of a posterior vena cava. D, Mammal; the renal portal eliminated, (Vessels of the right side are shown in deeper adming.)

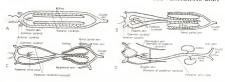


Fig. 321. Diagrams in ventral view to show the evolution of the posterior cardinals and the development of a posterior vena cava. Stages as in Figure 320.

recognized that common jugular and anterior vena cava are the anterior cardinals of lower vertebrates. In many mammals (including man) there is a further change (Fig. 318) by which the blood from the left jugular (or vena cava) is shunted across to the right side, so that only a single vessel enters the heart. A comparable development is seen in birds.

The story of the posterior cardinals is more complex (Figs. 320, 321). It begins with a pair of simple dorsal trunk vessels draining forward into the heart via the common cardinals; it ends in mammals with the draining of the same region by a single but complex vessel, the posterior vena cava. In between lies a considerable history.

In cyclostomes the posterior cardinals are simple paired vessels, receiving blood from the tail, kidneys, gonads, and dorsal parts of the body musculature and running forward uninterruptedly to the common cardinal region. In the sharklike fishes, however, there develops a renal pottal system, destined to persist upward into the reptilian stage. Blood from the posterior part of the trunk and the tail does not now go directly forward through the original cardinal channels, but is instead shunted through a network of capillaries around the kidney tubules, whence it resumes its forward course, through the cardinals.

In the Sarcopterygii, as exemplified by the lungfishes, a second progressive change initiates the development of a posterior vena cava. A branch of the he-patic veins of the liver here extends up past that organ in a mescnteric fold to the dorsal wall of the body cavity and taps the right posterior cardinal. Once this connection is made, blood from this cardinal follows this new short circuit to the heart; further, since there are cross-connections between the two cardinals, the blood originally following the left cardinal anteriorly likewise takes this course. The old channels persist in lungfishes and urodeles, but in frogs and all higher forms are abandoned (leaving only variable stumps termed the azygos veins). The new major trunk from kidney region to heart may be properly termed the posterior vena cave.

In land vertebrates the renal portal system shows some evidence of degeneration even in amphibians, more in reptiles; in birds it is in great measure abandoned and in mammals completely so. With this abandonment there occurs a bird major stage in vena cava development. The blood now passes directly forward from the back of the body past the kidneys, the whole channel along the trunk to the heart being the definitive posterior vena cava. This great single vein in adult mammals and birds has a seemingly simple structure. This is, however,

deceptive. The phylogenetic story shows, as we have seen, that it is a composite patchwork of the old posterior cardinals and vessels replacing them and, anteriorly, of an enlarged part of the hepatic vein system. The embryonic development of the mammalian circulation recapitulates this evolutionary story in an elaborate (if somewhat variable) fashion, as shown in Figure 319.

Abdominal Veins. In the sharklike fishes small paired abdominal veins run forward along the belly on either side, draining the flank musculature (Figs. 306, 316, A, pp. 320, 326). They are absent in actinopterygians. In lungfishes we find instead of paired vessels a median abdominal element. This persists in amphibians and reptiles, but instead of entering the heart directly it joins the hepatic portal blood in the liver sinuses (Figs. 307, 316, B). The area drained by abdominal veins is sometimes extended to include the pelvic appendages and tail. The vein is absent in adult birds and mammals, but, as noted later, it is of interest in the embryo, where it is represented by the important umbilical veins (p. 340).

Limb Veins. In tetrapods pectoral and pelvic limbs are drained by large vessels termed the subclavian and iliac veins. The former enters the anterior cardinals or their replacements, the jugulars or anterior vena cava; the latter rather variably connects in lower tetrapods with the abdominal vein or the renal portal system or both; in mammals the two lifac veins are the main elements which join to form the posterior vena cava. Much smaller veins, with variable connections, drain the paired fins of fishes.

# LYMPHATICS

In all except the lowest vertebrate groups we find, supplementing the venous system, a second series of vessels returning fluids from the tissues to the heartthe lymphatic system. Although paralleling the veins in many functions (and often paralleling them topographically) the lymphatics differ from them in major respects. A fundamental difference is that the lymphatics are not connected in any way with the arteries; they arise from capillaries, but these are blind at their tips. There is thus no arterial pressure behind the fluid in the lymphatic vessels, and the flow of materials in them is generally sluggish. This contained liquid, the lymph, diffuses into the lymphatic vessels from the general tissue juice and hence is generally similar in composition to this fluid and (apart from the absence of blood proteins) to the blood plasma. Except for white corpuscles which may enter by ameboid motion, there is, of course, no inflow of blood corpuscles. Abundant lymphocytes are found in the lymph nodes of mammals, but these nodes, we have noted, are almost completely absent in other vertebrate groups. Related to the low pressure under which lymph travels, lymphatics (Fig. 302) are very thin walled, and even the largest of them are difficult to find and dissect unless specially injected. Lymphatics are absent in cyclostomes and sharklike fishes; they are present in bony fishes and highly developed in tetrapods-most notably in amphibians. In this class lymph circulation is aided by the development of pulsating lymph hearts-small, two-chambered structures usually lying at points where lymph vessels enter the venous trunks. The major development of lymphatics in tetrapods may be due to the fact that blood pressure in the body capillaries is higher than in fishes; the lymphatics offer a relatively low pressure system of drainage of the tissues.

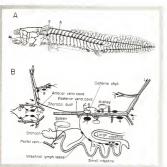


Fig. 322. A, Side view of a salamander, showing superficial lymph vessels, Dorsal, lateral, and ventral longitudinal vessels are present; a series of lymph hearts (h) is present along the lateral vessel. Lymph from this vessel enters the venous circulation through an axillary sac (a); lymph from the ventral vessel enters through an inguinal sac. B, Diagram of the deep vessels of the lymphatic system of the rat, anterior end at left. Lymphatics in solid black; the neighboring veins also shown. Nodes are numbered according to the region in which they lie: 1, knee; 2, tail; 3, inguinal; 4. lumbar; 5, kidney; 6, nodes about the cisterna chyli; 7, intestinal node; 8, elbow; 9, axilla; 10, thoracic; 11, cervical; 12, submaxillary; 13, mesenteric nodes; t, plexus of lymphatics around tongue and lips. Arrows indicate the point of entrance of lymph into the veins near the junction of jugular and subclavian and into the portal vein. (A after Hoyer and Udziela; B after Job.)

Lymphatics are prominently developed in the intestine, whence they carry (via the mesenteries) much of the absorbed fats in a milky liquid, the chyle, and in amphibians are particularly abundant in the subcutaneous tissues (Fig. 322). Lymph vessels are absent from the nervous system, liver, spleen and hone marnow. The arrangement of major lymph vessels varies greatly from group to group. They usually terminate at entrances into the cardinals or venae cavae; in higher tetrapods most or all of the lymph drains into the anterior venae cavae close to the heart (a point of lowest pressure in the circulatory system). The intestinal lymphatics usually run upward into a longitudinal thoracic duct, primitively paired but in mammals frequently reduced to a single vessel.

#### THE HEART

Some type of muscular pump is necessary for efficient circulation of the blood. Amphioxus has a whole series of tiny "heartlets," but in true vertebrates the heart is a single structure, situated ventrally and well anteriorly in the trunk. It sucks in venous blood posteriorly from all regions of the body and pumps it anteriorly, in lower vertebrates, to the aortic arch system and the gill circulation. Primitively it consisted of four successive chambers, termed, from back to front, sinus venosus, atrium, ventricle, conus arteriosus; in advanced groups the first and last lose their identity, but atrium and ventricle tend to subdivide.

The heart is situated in a special anterior and ventral region of the celom, the pericardial cavity, free from surrounding structures except at the points of entrance and exit of vessels, so that it is able to change its shape readily during its powerful pumping movements. The heart is essentially a series of expansions developed along the course of a main blood trunk, and hence is lined with

Fig. 323. Diagram of a mammalian heart opened from the ventral surface to show the conducting system. (From Carlson and Johnson, The Machinery of the Body, University of Chicago Press.)



an endothelium continuous with that of the blood vessels, surrounding which is muscle and connective tissue; externally there is a thin outer epithelium as in the case of any other organ lying in the celomic cavities. The musculature, of a peculiar strated type, which we have noted to be derived from tissues otherwise forming smooth muscle fibers, is especially thick around the ventricle (or ventricles), and on the other hand, is thin about the sinus venous, first of the four primitive heart chambers. Between the chambers and at the points of entrance or exit of vessels are heart rathes, basically similar to those in veins (and in lymphatics as well), but more powerful and usually of complex structure.

Fibers from the autonomic nervous system reach the heart (at sinus venosus or atrium) and may affect its rhythm; the heart, however, is essentially "on its own" as is shown by the fact that heart muscles will continue a rhythmic contraction even when cultured apart from the body. The contraction takes place in sequence, from back to front, through the four chambers of the primitive heart or, in advanced types, in the atria followed by the ventricles. The contraction of the musculature of one chamber (primitively the sinus venosus) induces stimulation, successively, of the muscle fibers of the remaining chambers of the heart. In aminotes—notably in birds and mammals—there develops a unique conducting mechanism, the sinoneutricular system of specialized muscle fibers which simulates a local nervous system (Fig. 323). Stimulation of a node in the right member of the pair of atria sets up contraction in these chambers; a second node is thereby stimulated and the impulse is carried via a bundle of fibers to the muscles of the ventricles.

The Primitive Heart. The heart of typical fishes is a single tube considering of four consecutive chambers. The heart of a bird or mammal likewise has four chambers, but these do not correspond to those of a primitive vertebrate; it is, rather, a double pump, with two chambers in each of its two parts. The great changes that have occurred in heart history are correlated with the shift from gill breathing to lung breathing.

In the more primitive vertebrate heart (Figs. 324, 325, A) there are present, in order: (1) sinus renosus, a thin-walled sac into which blood enters from the cardinals and from the hepatic vein or veins; (2) atrium (or auricle), still relatively thin-walled and distensible; (3) rentricle, the thick-walled major contrac-

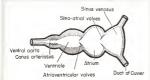


Fig. 324. Diagram of the chambers of the primitive vertebrate heart. (After Ihle.)

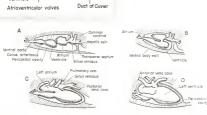


Fig. 225. Diagrammatic views of left side of heart in various vertexarts, to show its position in the pericential cavity and phylogenetic modification of the heart techniers. A. Bypothetic ancestral condition, fund osentially repeated in embryos (cf. Figurs 234). The four primitive chambers are to the amountaposteriority, and a docal measurery is still present. B. Schwinin stage: the measurery is poser, the stream has pushed forward above the ventricle, but the simulation was still posteriority placed. C. Ampilian stage; the sinus and accompanying blood vessels have moved autoritority. B. Aumitot stage, sinus and couns arterious have lost their identity; the heart attaches to the walls of the perioritorium only auternots.

tile portion of the heart; and (4) conus arteriosus, a narrow but stout tube leading to the ventral aorta, frequently furnished with several sets of valves. In the embryo these four chambers are arranged in an essentially straight line from back to front. But during development the front part of the heart tube tends to fold back ventrally in an S-shaped curve, thus combining length with compact structure (Fig. 325, B-I). As a result, even in a fish heart, the more "posterior" chambers tend to be situated dorsal, or even anterior, to the "anterior" ones. (This makes visualization of heart construction difficult, and in diagrams Jas Fig. 311] the heart is often represented as if "pulled out" into its embryonic longitudinal arrangement.)

Evolution of the Double Heart Circuit (cf. Fig. 311, p. 322). The primitive type of heart described above is present in most fishes. In lungfishes, however, and more fully in amphibians, a major difficulty arises with the substitution of lungs for gills as breathing organs. The heart now receives blood of two different types: "spent" blood from the body and "fresh," oxygenated blood from the lungs. The two streams should be kept separate, as far as possible, and sent

to two different destinations—venous blood to the lungs, "fresh" blood to the body—by separate aortic trunks. But how to keep the two separate in a singlebarrelled pump?

A good solution of this difficulty was not attained until the avian and mammalian stages were reached, but lungfishes and amphibians have made some progress toward separation of the blood streams. Even in lungfishes, the pulmonary vein does not enter the sinus venosus like the other venous trunks. Here and in amphibians (Fig. 326, 4) the atrium is divided into two halves, the pulmonary vein entering the left portion. The "spent" venous blood enters the right half of the atrium; the sinus venosus, which leads to this chamber, is reduced in size in some ambibians (anurans) and is merged with it in amniors.

Buf atrial separation is in vain if the two streams meet and mingle in the ventricle. A variety of adaptations in lungfishes and amphibians prevent complete mixture of the two, but much blending nevertheless occurs. It is only in amniotes that the two streams come to be effectively separated by subdivision of ventricle as well as atrium into two parts. In most reptiles there is a ventricular septum, but it is incomplete and some admixture still takes place. In crocodilians the ventricular septum itself is complete but there is still a gap at the base of the arterial conus. In lower tetrapods and even in lungfishes there is seen, however, some tendency for subdivision of the conus. In birds and mammals this division is completed; the conus is done away with as a separate structure and at long last in the evolutionary series the two blood streams of the heart are completely separated (Fig. 326, B).

The introduction of the lung into the blood circuit in advanced fishes three out of order the simple heart plan of primitive vertebrates and furnished a "problem" which advanced vertebrates found difficult to solve. Lungfishes, amphibians and reptiles even today have not solved it completely, although their partial solutions are satisfactory enough to allow them to survive. In binds and mammals alone is the complete solution seen and complete separation of circuits attained. The result is surprising in its efficiency. The single pump of the original heart has become a double one; each half of the heart performs effectively its own distinct task.

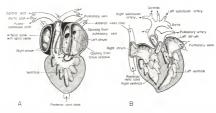


Fig. 326. Diagrammatic section through the heart of A, a frog; B, a typical mammal. (Partly after Jammes.)



Fig. 327. Cross sections of a mammalian embryo to show an early stage in heart formation, before the fusion of the two subintestinal vessels from which the heart forms. In the atrial region, 4, the two are still widely separated; farther forward, in the ventricular region, B, the two tubes are apposed inside a single pericardual sac, but are not yet fused. (From Ares).

Heart Development. We have noted that the first blood vessels to develop in the embryo form a subintestinal vein running forward from gut to gill arch region. The heart forms along the course of this vessel. Particularly in forms with a large yolk, in which the animal has at first no formed ventral surface, this vessel may long persist in the embryo in the form of paired vitelline veins, and the pulsating region which is to form the heart may at first be a paired structure (Fig. 327, 4). About the early heart tube develops a portion of the celomic cavity, and in all vertebrates there presently occurs the S-shaped curvature of the heart tube and its subdivision into a series of chambers. The higher vertebrates show further development, with a gradual subdivision of atrium and ventricle and absorption into them-of atrium and couns arterious; these stages, as seen in a mammal, essentially recapitulate the phylogenetic history of the mammalian heart.

#### BLOOD CIRCUITS

In earlier sections of this chapter the components of the blood circuit have been described piecemeal. We shall here briefly review the general evolutionary history of the circulation as a whole with especial reference to blood pressures and capillary nets (Fig. 328).

As in any passage of liquid through tubes, the friction of the liquid on the walls tends to lessen the pressure given by the "pump," and the capillaries are, of course, the parts of the system in which the fall in pressure is the greatest. In fishes, in general, every drop of blood leaving the heart must pass through at least two capillary systems before returning to the heart—first in the gills, then in the general body tissues. Much of it, however, must pass through at bird capillary net as well, for that which has gone to the gut must pass through at the hepatic portal, that to the tail must on return pass through the portal system of the kidneys. The nature of the fish circulatory circuits thus makes heavy work of the maintenance of blood pressure. With the introduction of the lung circuit and the abolition of gill capillaries in adult tetrapods, circulatory efficiency is greatly promoted. All body tissues are reached directly and with little loss of pressure. Two capillary systems only, not three, are encountered by blood traversing the hepatic portal or the renal portal of lower tetrapods, and the general body circulation passes but a single capillary net instead of two. The substitution of lungs

CIRCULATORY SYSTEM 337

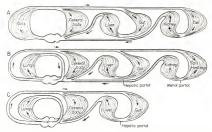


Fig. 328. Diagrams showing the general nature of the blood circuits and capillary networks encountered in A. a typical fish; B. a terrestrial amphibian or a reptile, with elimination of gill circulation and introduction of pulmonary circuit; C. a mammal or a bird, with elimination of renal portal system.

for gills has brought about, in the long run, not only an improved heart but also a circulatory system more generally efficient. With reduction in amniotes of the renal portal system there is further increased efficiency; in birds and mammals it is only the intestinal circulation that encounters two capillary networks.

# EMBRYONIC CIRCULATION

In earlier sections of this chapter we mentioned the formation of this or that blood vessel in the embryo. Although nessearily involving some repetition we may here attempt to gain a general picture of the development of the circulatory system, with attention to some of the vessels not present in the adult but necessary in the embryonic structures of forms with large-yolded eggs. It must be emphasized that the circulatory system cannot develop in the embryo merely with the "aim" of producing adult structures; it must be functionally effective at every moment of every embryonic or larval period. In general, too, we may note that in many areas (as in the limbs, Fig. 329) the circulation first develops in the form of a diffuse network, from which major vessels are "sorted out" only at a later stare.

The most generalized embryonic pattern is that developed in such forms as ungfishes and amphibians (Fig. 330), in which the picture is not complicated by excessive yolk or accessory membranes. Most of the nutriment on which the embryo must depend before feeding occurs lies in the yolky cells of the gut floor, and the first vessels arise there, forming a pair of vitelline seins which unite anteriorly into a subintestinal vessel. Along the course of this trunk the heart devoleps; the authoritor end becomes the ventral aorta. Back of the heart the region of the subintestinal trunk is later invaded by liver tissue; the vessel is divided into the hepatic vein or veins anteriorly and the hepatic portal posteriorly, with a system of liver sinusoids between the two. At the front end of the body the trunk meanwhile has divided to curve puward on either side of the pharynx to



Fig. 329. An early stage in the development of the forcitimb of a pig embryo, to show the manner of formation of patterns in limb circulation. There is a network of interveaving small yessels from which the main adult vessels develop. Choice of one definitive channel or another allows for the occurrence of variants as anomalies. (From Woolard.)

form the first of the aortic arches; we have previously described the successive development of further arches more posteriorly and the usual degeneration of those first formed. Dorsally the major blood flow of the early embryo continues backward to form the dorsal aorta, paired anteriorly but further back forming a single median vessel below the notochord and above the gut tube and colon. Much of the blood from the aorta courses downward in vitelline arteries, corresponding in general to the celiac and mesenteric arteries of the adult, to reach the gut floor again and complete a primitive circuit.

But part of the aortic blood does not follow this path; instead, it leaves the aorta to supply the growing musculature of the body walls, the nervous system and other structures of the outer tube of the body. A return system must be created for this blood. This is effected by the development of paired cardinals (Fig. 331) which develop the length of body and head, one on either side of the

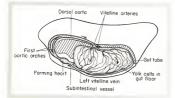


Fig. 330. Diagram of the general circulation in a young frog tadpole. The food supply still lies in the yolky gut cells, and the vitelline circulation is of great importance.

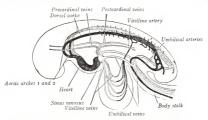


Fig. 331. The circulatory vessels in a mammalian embryo. (From Arey, after Felix.)

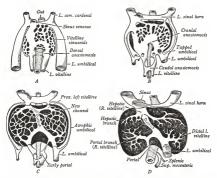


Fig. 332. Diagrams of the liver region of human embryos at successive stages (5.5, 5.6, ad.90 mm, in length), sere from the ventral surface, so show developmented changes in the visitlen and umbilical visins. (The gat tube is stippled.) In A the vitefline vossels from the yulk as are well developed and pass through the liver tissue; in B B their transformation into the portal system is seen. The umbilical vents from the placental) are already well developed in A, but run directly to the sinus venous. In later stages this blood from is diverted to the five circulation, much of if thosing through this organ via a heptic duct. The distribution will be the side of the vice circulation, much of if thosing through this organ via a heptic duct. The foundation of the organization of the post of the circulation of the organization of the circulation of the organization of the circulation of the organization of the organization

dorsal aorta. At a point above the heart each vessel sends a trunk, the common cardinal, down along the body wall to reach the heart. In all vertebrates above the cyclostome level the renal portal system is presently developed by interruption of the posterior cardinals. There is now established a general pattern of circulation which needs only few additions of any importance to attain adult conditions except for introduction of a circuit to and from the lungs in forms possessing these structures, and for development of limb circulations.

The presence of a large amount of yolk and the development of a yolk sac in sharklike fishes and amniotes give a different appearance to the embryonic blood circuits (Fig. 331). The basic pattern is, however, the same as before. The nutrient yolk now lies not in the floor of a closed gut tube but in a large pendant sac. In consequence the vitelline veins, highly developed, arise over the surface of the expanded yolk sac; the vitelline arteries are equally highly developed and extend outward onto this sac, paralleling the veins.

In amniotes the addition of the allantois makes a further complication in the picture. In reptiles and birds this forms (with the chorion) a breathing organ, and vessels develop in the allantoic stalk for the necessary blood supply. These are the allantoic arteries and allantoic veins; the term umbilical, however, is generally used for them in mammalian studies, since they are the important vessels in the umbilical cord of the fetus. The allantoic arteries descend through the body walls to the allantoic stalk from the back end of the dorsal aorta. The corresponding veins (which may fuse for most of their course) do not, however, join the subintestinal "circuit," as one might expect. Instead, they run forward in the lateral body wall on either side, and thus correspond to the abdominal veins of a shark. In early stages they enter the common cardinal or sinus venosus directly (Fig. 332, A). Later, however, they turn upward to pass through the liver tissues; apparently the liver sinusoids are unable to care for the entire flow of blood and much of it in the embryo may pass through the liver tissue by way of a large duct (Fig. 332, C, D). In mammals these same vessels carry not only oxygen but food from the placenta and hence are of the highest importance.

In all forms with a yolk sac, the vitelline vessels leading from it are resorbed when the sac contents are exhausted. In placental mammals, as we have noted, the yolk sac contains no food and the vitelline vessels disappear at an early stage. At hatching or at birth the allantoic (or umbilical) vessels likewise disappear.

Among tetrapods there is a marked circulatory change due to a change in oxygen source when lungs become functional—at metamorphosis, hatching or birth. Up to that time there is little circulation of blood through the pulmonary arteries or veins. We have noted that on the arterial side of the circuit the retention of the ductus arteriosus allows blood in the pulmonary arch to bypass the lung. If, in amniotes, the two stria were separated in the embryo (as in the adult) by a partition, the left side of the heart would remain empty, since there is no blood entering from the pulmonary veins. In consequence, even in birds and mammals, gaps are present in the ventricular wall of the embryo's heart. When the lungs begin to function, there is a rapid and efficient shift in these features. The ductus arteriosus closes, the full pulmonary flow passes through the lungs and back to the heart, and, in birds and mammals, the gaps in the septum between the ventricles rapidly close.

# 15

# SENSE ORGANS

All cells, one may believe, are capable of receiving and responding to stimuli that measure, so to speak, some condition in the environment or a change in such condition. If, however, in a vertebrate the proper response to a sensory stimulus is one that should be performed by a distant region of the organism, or by the organism as a whole, its reception is in vain unless there is some channel of communication between the sensory recept and the organism—muscles or glands—which should make the appropriate response. Such communication may be made by bormonal action, but in general the mechanism used is that of the nervous system. The tips of nerve fibers are themselves capable of direct excitation, but more often the reception of sensation in vertebrates is the function of specialized sensory cells, generally grouped in organs of lesser or greater degree of complexity. These are attuned to physical or chemical stimuli of specific types and are associated with nerves which relay these stimuli to specific centers in the brain or to the nerve cord.

Anatomists divide such nerves, sensory in nature, into two groups: the somatic sensory nerves, carrrying impulses of a sort which in ourselves usually reach the level of consciousness, from the "outer tube" of the body—the skin and body surfaces and the muscles; and visceral sensory nerves, whose impulses; seldom reaching our consciousness, arise from the viscera. The physiologist customarily classified sensory receptors in a fashion which fits readily into the neurologic scheme. Extreoepotors are those sensory structures of the skin and special senses which receive sensations from the outside world; proprioceptors include those situated in the striated voluntary muscles and tendons, interoceptors are those located in the internal organs. The first two of these correlate fairly well with the somatic system of sensory nerves, the third with the visceral sensory system of the anatomists.

# SIMPLE SENSE ORGANS

gan for its reception but may be produced by direct stimulation of the end fibers of sensory nerves. Particularly in lower vertebrates, other simple sensations may to some degree be received directly by excitation of nerve endings.

Sense Corpuscles. In all vertebrates, but most notably in mammals, a variety of sensations are received by small sensory structures, generally of microscopie size, which may be present in any part of the body—in skin, muscles, or viscera. These are relatively rare in lower vertebrates but abundant in birds and mammals. Their appearance and structure vary greatly (Fig. 333). It is of course, difficult to determine the specific functions of many of these structures, but from our own experience it seems that at least four types of simple sensations can be registered by such bodies—warmth, cold, touch and pressure. Proprioceptive sensations, of the physiologistic terminology, include those of the muscle spindles (Fig. 334) and tendon spindles. In lower vertebrate classes terminal nerve fibris may twist about individual muscle fibers or sproad among tendon fibers. In man-

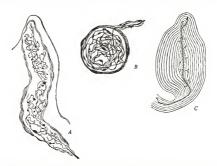


Fig. 333. Some types of sensory organs from marmmalian tissues. A. Tactile corpuscle (Meissner's corpuscle) from the connective lissue of the skin; B, an end bulb of Krause, sensitive to cold; C, a paconian corpuscle, which registers pressure and tension. (From Ranson, after Dogiel, Sala, Bohm-Davidoff, Huber.)



Fig. 334. A muscle spindle. (After Windle, Textbook of Histology, McGraw-Hill.)

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mals there are specialized receptors, the spindles, which consist of a group of small muscle fibers surrounded by a maze of sensory nerve endings and enclosed in a sheath. These receptors are the seat of "muscle sense." They not only register the state of contraction of the muscle concerned but (amazingly) give information as to the position in space of various parts of the body—information, as we are ourselves well aware, which can be furnished without the aid of other sensory structures, but strictly confined (in the absence of contact with other objects) to parts of the body containing striated muscles or tendons.

Tasie. In contrast to the simple senses named above, taste and smell are responses to chemical stimuli, the former received by taste buds—small barrel-like collections of elongate cells sunk within an epithelium (Fig. 335). The "staves" of the barrel are supporting cells, in the center are the taste cells proper, elongate and tipped externally with a sensitive, hairlike process. Although for the most part confined to the mouth, and in mammals concentrated on the tongue, they may be more widely distributed, and in fishes and amphibians may be found in the skin. In some catfishes, for example, they are widespread over the entire surface of the body, giving a phenomenal possibly of pleasant (or umpleasant) gustatory sensations. It must be noted that much of what we casually think of as taste is actually a smelling of mouth contents (foods do not "taste" as well when a head cold clogs the nose). All taste buds look alike, but there appear to be four types, as regards reception, giving sensations of salty, sour, bitter and sweet.

In sections which follow are described the more prominent of the complicated sensory structures of vertebrates—none, eve and  $\alpha_{\rm r}$ , and the lateral line organs of fishes. Very probably, however, there is a variety of still further sensory structures, particularly in lower vertebrates, which give responses of types unfamiliar to us and hence difficult for us to understand. One such sense, about which we do not have data, lies in the pit organ of the so-called pit vipers. Placed between eye and nose, and filled with vascular itsues and nerve endings, the pit is highly sensitive to the movement nearby of a warm body of any sort—a sensory power extremely useful to such an animal as a rattlesnake which

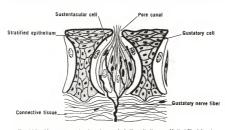


Fig. 335. Microscopic section through a taste bud. (From De Courcey, Medical Physiology.)

makes its living by capturing warmblooded rodents and is not too well endowed with "normal" sense organs.

### THE NOSE

In tetrapods the nose has become associated with breathing, but its primary function is that of olfaction—the detection of minute amounts of chemical particles received from objects at a distance and the "sorting out" of these sensations into a variety of categories which are still poorly understood. In certain verterbate groups smell is relatively unimportant; it is not generally highly developed in teleosts and is rather feeble in most birds, in marine mammals, and in higher primates, including man. In vertebrates generally, however, smell is in many ways the most important of all the senses; testimony to its importance is the fact that, as we shall later see, the most highly developed brain centers arise in an area primarily connected with smell.

In most fishes the nasal structures consist of a pair of pockets, placed well anteriorly in the head and without an internal opening to the mouth; cach pocket has two openings, partially or completely separated, allowing a flow of water through the cavity beneath. In most bony fishes the nostrils are lateral in position; in sharks they lie beneath the snout. Within the nasal sace is a highly folded epithelium of simple columnar type, containing olfactory cells interspersed with supporting elements (Fig. 336). On its exposed surface each olfactory cell bears a radiating brush of short, hairlike sensitive processes. In one remarkable feature—very probably primitive—these cells differ from any other vertebrate receptors. All others depend upon nerve fibers to relay inward the sensations received. The ol-factory cells, on the contrary, do their own work; a long fiber extends from the cell itself inward to the brain.

The jawless vertebrates present a puzzling situation. In contrast to all other living vertebrates, the olfactory organ in cyclostomes is a single median pouch, opening at the tip of the snout (hagfishes) or high atop the head (lampreys); as a further peculiarity, it is combined with the hypophyseal sac (Figs. 17, 231, pp. 37, 247). Is this condition primitive or specialized? The answer is none to the properties of the prop



Fig. 336. Section through the nasal mucosa. (From De Courcey, Medical Physiology.)

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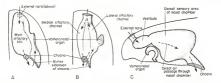
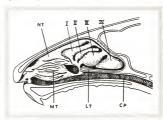


Fig. 337. A. Ventral view of anterior part of the left side of the palatal region of the salamander, Triton, with the assal channels shown as solid objects, remainder as transparent structures (cf. Fig. 208, a.p., 231), B. Similar view of the total Pips. C. Longinatinal section of the assal regions of a lizard, cut somewhat to the right of the middline, to show the cavities of the assal apparatus, in the endryo lizard the vonecrosus organ was a lateral pocket of the main assal channels, as in an amphibiari in the adult (as in many marmially this organ has separated to open independently into the roof of the month by an apulation duct. Arrows show the main air flow inward in all figures and the outward flow toward the vonecrosus organ in the amphibiasis, (A flow Matthew S after Bascorife, C after Leeding, 1).

clear. In some (but not all) of the most ancient fossil vertebrates, the nostril is comparable to that of a lamprey; on the other hand, the lamprey nostril is in a more normal ventral position in the embryo and is bilobed, although not distinctly paired, in the lamprey larva.

In the typical crossopterygians there evolved a type of nostril with an opening into the roof of the mouth as well as to the exterior. In the tetrapods this passage is utilized as an adjunct to breathing. Here the olfactory pouch is filled with air rather than water, but nasal glands and liquid brought from the eye by the tear duck keep the sensory epithelium moist and capable of functioning. In this new type of nasal apparatus the structure is at first simple. In amphibians (Fig. 337, A, B) an external naris leads into a somewhat elongated sac; posteroventrally, a large opening, the choana, or internal naris, opens directly from this into the front part of the roof of the mouth. The inner surface of the sac is nearly smooth, and only part of its lining is sensory.

Fig. 338. A section through the nasal region of a guinea pig, slightly to the right of the midline, to show the development of the turbinals, including the maxilloturbinal, MT. nasil turbinal, NT, and ethmoturbinals (I–IV). CP. Choanal passage; LT, lamina transversalis separating sensory area of the nasal fossa from the choanal passage. (After Cave.)



In typical reptiles the nasal region begins to assume a more complex structure (Fig. 337, C). The air passage is longer, there is usually a small but distinct vestibule anteriorly, and the sensory epithelium is confined to the upper part of the main chamber. Here there is typically developed one or several curved in growths from the lateral wall as conchea or turbinals, increasing the epithelial area. In certain turtles, as we have noted previously, there is some development of a secondary palate; in crocodilians this is greatly elongated, with a related development of a tube leading backward above it from the nasal chamber. In birds, generally, smell appears to be of very little importance and the nasal structures, built on the general reptilian plan, are of modest size.

Nasal structures reach the peak of their development among mammals (Fig. 209, p. 232; 388). In typical members of the class (higher primates are exceptional) the nasal chamber may reach back to the orbits to occupy as much as half the skull length. The conchae are usually highly developed, increasing the old factory area in the upper part of the chamber and acting as ir filters and "conditioners" in the direct air passage below. Back of the main chamber there is present, as in crocodilians, a tube—the naspharyngeal duct—carrying the air back above the secondary palate to the pharynx. In placental mammals there are present extensions of the nasal air spaces into the adjacent hones as the sinus pneumatici (plural) which effect a lightening of the skull (and have other effects perhaps all too familiar to some readers).

In numerous tetrapods there is a specialized part of the olfactory system termed the comeronasal organ or organ of Jacobson which appears to have as its main function the picking up of olfactory sensations from the food in the mouth. In urodeles (Fig. 337, 4) there is simply an area of sensory epithelium lying in a channel somewhat distinct from that carrying inward the main current of air. In the other amphilibans and in repitles the organ is placed in a blind pouch lying to one side (Fig. 337, B). This appears to be the primitive reptile condition, as seen in Sphenodon. In lizards and snakes, however, (Fig. 337, C) the two vomeronasal organs come to occupy a pair of pouches which open quite separately into the roof of the mouth. A peculiar development is seen in many lizards and snakes. The tongue, cleft into two prongs and darting in and out of the mouth, serves as an accessory olfactory organ. When the tongue is withdrawn, the tips are inserted into the vomeronasal pockets, chemical particles which adhere to them in the air are transferred to the moisture on the sensory epithelium of these pouches.

The organ is absent in turtles, crocodilians and birds, and also in some mammals (such as higher primates). Other mammals, however, have retained it; in rodents it opens into the main nasal cavity but in other forms which retain it, there are separate openings, as in lizards and snakes, into the roof of the mouth cavity.

#### THE EYE

The vertebrate body is subjected constantly to radiations which may vary from the extremely short but rapid waves of cosmic rays and those from atomic disintegration to the long, slow undulations utilized for radio transmission. Many of these affect protoplasm, but specific sensitivity appears to be limited to a narrow band part way between the two extremes; for knowledge of other wavelengths we must resort to mechanism which transform their effects into terms receivable SENSE ORGANS 347

by our own limited senses. It is not unreasonable to find that the animal band of sensitivity corresponds in great measure to the range of radiations reaching the earth from the sun, since that hody is the source of the vast bulk of the radiations that normally reach us. Of this band, the slower waves are received as beat, the faster, shorter waves perceived as light—the process of photoreception.

Specific sensitivity to light is widespread throughout the animal kingdom, many simple invertehrates there develop "eye spots" as sensitive cell clusters, frequently with associated pigment, and often there is an evolutionary progress to an organized eye structure, with a lens for concentrating light upon sensitive cells in a closed chamber. Many simple eyes merely receive light "in bulk!", with better organization and the arrangement of sensory cells in a definite pattern so as to receive light from specific external areas, true vision results. Well developed eyes, with many common features, but surely independently evolved, are found in forms as far apart as molluses, arthropods of various sorts, and vertebrates.

In the vertebrate eye, the essential structure (Figs. 339, 340) is the roughly spherical eyebull, situated in a recess, the orbit, on either side of the braincase, and connected with the brain by an optic nerve, contained in a stalk emerging from the medial surface of the eyeball. The eyeball has an essentially radial sym-

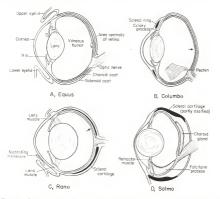


Fig. 339. Diagrammatic vertical sections through the eye of I, a horse: B, a dove: C, a common frog. B, a teleous (salmon). Connective tissue of sclera and cornea unshaded; scleral ring or cardinge black; choroid, ciliary body, and iris stippled; retina hatched. Arrows point to the force, In B is shown the pertent, lying to one side of the midline. In D the section is slightly to one side of the choroid insure through which the factoring proves enter the eyeball, (After Rocho-Duvigeaud, Walls.)

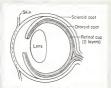


Fig. 340. Diagrammatic section of an eye to show the arrangement of the successive embryonic layers.

metry, with a main axis running from inner to outer aspects. Within it is a set of chambers filled with watery or gelatinous liquids. In the interior, well toward the front, lies a lens. The walls of the hollow eyeball are formed basically of three layers, in order, from the outside inward, the scleroid and choroid coats and the retina. The scleroid is a complete sphere; choroid and retina are incomplete externally. The first two are of mesenchyme origin and are essentially supporting and nutritive in function; the retina (actually a double layer) includes the truly sensory part of the eye system. At the outer end of the eyeball the scleroid coat is modified to form, with the overlying skin, the transparent cornea. Toward the exterior, choroid and retinal layers are fused and modified. Opposite the margins of the lens these conjoined layers usually expand to form a ciliary body, from which the lens may be suspended. Forward beyond this point the two fused layers curve inward parallel to the lens to form the iris, leaving a centrally situated opening, the papil.

The operation of the eye is commonly (and reasonably) compared to that of a simple box camera. The chamber of the eyeball corresponds to the dark interior of the box; in both a lens focuses the light properly on a sheet of sensitive materials at the back of the chamber. The iris of the eye is comparable to the similarly named diaphragm of the camera in regulating the size of the pupil.

Development (Fig. 341). Embryologically, the most important functional parts of the eyeball arise from the ectoderm (including neuroctoderm), but mesenchyme also enters prominently into the picture. At about the time of completion of the brain tube there grow outward on either side from the forebrain area spherical optic exietles, which remain connected by a stalk with the brain. As each vesied develops its outer layer folds into the inner to form a double-layered optic cap (in which, however, there may long persist a ventral fissure for entrance of blood vessels). The optic cup becomes the retina, which is thus a two-layered structure; from the retina come part of the ciliary body and iris.

As the optic vesicle grows out toward the surface, the overlying ectoderm thickens, and a spherical mass or pocket of this tissue sinks into the orifice of the cup to form the lens. In many (but not all) forms in which eye formation has been studied experimentally, it has been demonstrated that the stimulus for lens formation is provided by the approach of the optic vesicle to the ectoderm. Further eyeball structures are contributed by the mesenchyme: first an inner sheathing layer, primarily vascular, surrounds the retina to form the choroid coat; then an external sheath of connective tissue forms a complete external sphere as the seleroid coat (selerar) and comea.

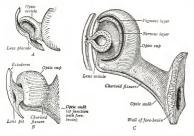


Fig. 341. A series of diagrams to show the embryonic development of the optic cup and lens. (From Arey.)

Sclera and Cornea. The scleroid coat is a stiff external structure which preserves the shape of the eyeball and resists pressures—internal or external—which might modify its shape. In cyclostomes, on the one hand, and mammals on the other, it consists entirely of dense connective tissue, but in most other groups it is reinforced by cartilage or bone. Often there is a cartilagionso cup (ossified in some birds) enclosing much of the back of the eyeball, and further protection may be afforded by a sclear irng of bony plates lying in the sclera in front of the "cquator" (Fig. 342). Fossil evidence shows that such a ring was present in primitive vertebrates of every major type, but it has persisted to the present only in actinopterygian fishes, repitles and birds. Primitively it appears to have consisted of four plates, but modern ray-funned fishes generally have but two, while reptiles and birds, or the other hand, have a much greater number of plates.

The superficial part of the eyeball is the translucent comea, through which light enters the eyeball. In all vertebrates above the eyelostomes the scleral coat fuses inseparably here with the overlying skin; this skin component of the cornea and the sensitive skin area beneath the lid folds constitute the conjunctiva. The refractive index of the cornea—that is, its ability to deflect the course of light waves—is practically the same as that of water. In air, however, the cornea itself acts as a lens and relieves the true lens of much of the task of focusing; its im-

Fig. 342. A skull of a bird (Aquila), showing the scleral ring in place. (From Edinger.)



portance is shown by the fact that in ourselves major defects calling for optical correction, such as astigmatism, are due to imperfections in corneal shape.

Choroid. This inner sheath of the eyeball contrasts strongly with the selera, for it is a soft tissue, rich in blood vessels supplying the retina. Pigments in the choroid absorb most of the light reaching it after penetrating the retina. In addition, there often develops here a light-reflecting device, most familiar to us assen in the ghostly eyes of a night-prowling cat illuminated by automobile beadlights. This is the tapetam lucidum, which may be formed either of a layer of glistening connective tissue fibers or a sheet of tissue filled with crystals of guantine (cf. p. 132). In nocturnal forms or in fishes living deep in the water, this structure is of use in "conserving" the sparse light rays, turning those otherwise wasted back to the retina.

Iris. This structure, found in all vertebrates, is formed by a combination of modified segments of both choroid and retinal layers, which, in attenuated form, join to furnish a pigmented diaphragm in front of the lens. This regulates the size of the pupil and, thus, the amount of light admitted through the lens to the retina. In some fishes the iris is fixed in dimensions, except when affected by movements of the underlying lens. But in sharks, in some teleosts, and in tetrapods, muscle cells are generally present; arranged in circular and radial patterns, they may expand or contract the pupillary opening, giving the effect of a camera daphragm in opening widely in dim light, "stopping down" the opening in bright light for better definition. The muscle fibers of the iris are formed from its retinal component, which is a derivative of the neural ectoderm of the embry. Orthodoxly, muscle is supposedly formed by the mesoderm. However, these cells in the iris have all the attributes of muscle fibers, structurally and functionally. The embryo eye has never read a textbook on embryology and in its innocence violates the rules laid down for it.

The Lens and Accommodation. In land vertebrates light rays are bent by the cornea, which consequently does much of the work of refraction, the lens merely acting as a "fine adjustment" for focusing. In fishes the cornea does not function in this way, and the entire task of focusing is hence performed by the lens itself. In consequence we find that in fishes the lens is spherical in shape and situated far forward in the eyeball, thus giving the lens maximum power and he longest possible distance for convergence of rays on to the retina; in tetrapods the lens is much less rounded and situated farther back in the eye cavity. The lens is formed of elongated collagen fibers arranged in a complicated pattern of layers; it is completely transparent, firm in shape and, in lower vertebrates, resistant to distortion. In cyclostomes the lens has no peripheral attachments and is kept in place merely by pressure from the "sirroous humon" behind it and the cornea in front; in all other vertebrates it is attached peripherally by a "belt," or zounle, of some sort, either a membrane or a radially arranged series of fibers,

As every user of a camera is aware, it is impossible to obtain exact "definition" of objects at varied distances without adjustment of the lens focus. Such adjustment in the eye is termed accommodation. The eyes of most vertebrates are capable of accommodation, but, curiously, it is attained in a different fashion in almost every major group. This suggests the probability that accommodation was not a property of the primitive vertebrate eye, and that different types of vertebrates have evolved this power independently of one another. The methods used may be broadly classified as follows:

- A. Lens moved:
  - Fixed position for near vision; moved backward for distant objects (lamprey, teleosts)
  - Fixed position for far vision; moved forward for near objects (elasmobranchs, amphibians)
- B. Shape of lens modified; fixed form for distant objects, expanded shape for near objects (amniotes)

It would be impossible to give in any limited space an account of the various special muscular developments used in these methods of accommodation. Movements of the lens are accomplished by the pull of variously developed muscles. Among the amniotes, the lens is made more rounded in repities and birds by the push against its margin of pads developed by the ciliary processes. In mammals the lens is "normally" kept in a relatively flattened condition by a pull on its margins of fibers connected with ciliary muscles, typically in a contracted state; when the muscles are relaxed, the elastic lens, released from tension, takes a more rounded shape. The amniote methods are effective only if the lens retains its elasticity. In man, as older persons know, it stiffens with age, accommodation diminishes, and without artificial aids a book can be read only at arm's length, if at all.

Cartites of the Eveball. Much of the cychall is, functionally, menely, a blank space which need only be filled by liquid—"humors"—which will not block or distort light rays. The principal eavity of the cychall, between lens and rettina, is filled by the thick, lell-ylike nitroos humor. In front of the lens is the aqueous humor. The cavity filled by it between comea and iris is termed the anterior chamber is not, as one might think, that filled by the vitroous humor, but the narrow area occupied by the aqueous humor between iris and lens (Fig. 343). A curious projection into the cavity of the vitreous humor in birds is the comb-like peeten (Fig. 339, B, p. 347). This structure is thought to have a nutritive function, but it has been suggested further that the "shadows" of the peeten ridges, falling on the retina, act as a grille ruling

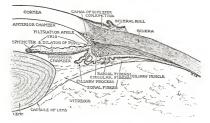


Fig. 343. Details of the outer segment of the human eye. (From Fulton.)

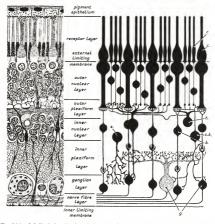


Fig. 344. Left, Vertical section through the retina of a mammal; Right, retinal connections are revealed by silver imperguation. a and h, Nervous elements of more or less uncertain function. Other abbreviations: b, bipolar cells associated with single cones; ε, cones, εb, bipolar cells, connecting with a series of rode; g, ganglion cells; τ, rods. (From Walls, partly after Polyak.)

which enables a bird more readily to detect small or distant moving objects as their images pass from one component to another on this grille.

Retina. All other parts of the eye are subordinate in importance to the critia; their duty is to see that light rays are brought in proper arrangement and focus to this structure for reception and transfer inward to the brain of the stimulation caused. In the adult the two layers of the retinal cup are fused. The outer one is thin and contributes little but a set of pigment cells; the complex sensory and nervous mechanisms of the retina all develop from its inner portion. Details of retinal structure vary greatly from form to form and from one part to another of a single retina. Frequently, however, a sectioned retina has the general appearance seen at the left in Figure 344. Inside the pigment layer (which adjoins the choroid) is a zone showing perpendicular striations; inside this again, are three distinct zones containing circular objects recognizable as cell nuclei. Appropriate staining reveals the true nature of these zones. The striated zone con-

tains the elongated tips of the light-receiving cells, the rods and cones; the outer nuclear zone contains the cell bodies and nuclei of these structures. The middle nuclear zone is that of bipolar cells which transmit impulses inward from the rods and cones, and of accessory types of retinal nerve cells. The innermost nuclei are those of ganglion cells which pick up the stimuli from the bipolar elements and send fibers along the optic nerve to the brain.

The rods and comes, whose names derive from their usual shapes, are the actual photoreceptors, each cell including a sensory tip directed toward the choroid, a thickened section, and a hasal piece containing the nucleus. One is immediately impressed by the fact that rod and cone cells in the vertebrate retina are "pointing the urong usay". In a "logically" constructed retina, their tips should point, not away from, but toward the light source. Some invertebrate eyes are so constructed; not those of vertebrates. This anomalous type of construction may be due to the retinal cells having first developed, phylogenetically, in the floor of the brain cavity with their tips facing inward (and upward) to catch light rays entering the translucent body of a primitive chordate from above, when they were transferred to outfolded optic vesicles, these cells simply retained their original orientation. Light reception in both rods and cones appears to be due to the momentary breakdown, when "hit" by light rays, of molecules in solution (rhodopsin, etc.) of a bluish to purplish or reddish tinge, which are compounds related to vitamin A.

Rods and cones differ markedly in function, as one can determine in his own eyes, where the cones are concentrated in the center of the field of vision, the rods situated, in the main, peripherally. (1) Rods are effective in faint light; cones come into play only with good illumination. At night one can often catch a glimpse of a faint star in the margin of the field of vision, but fail to see it if looking directly at it. (2) Cones as a group give good visual detail, rods a more blurred picture. For accurate vision we focus the cone-bearing center of the eye on the object. (3) Cones give color; rods give black-and-white effects only. In one's visual field, peripheral objects are gray and colorless.

We are ignorant of the reasons for the different "thresholds" to light of rods and cones. The reason for differences in perception of detail are pointed out below. As regards color, turtles and birds have colored oil globules in their cones which may act as filters and thus give differential reception to colors, but in other

vertebrates all cone cells appear to be structurally identical.

The distribution of rod and cone cells in the various vertebrate groups is highly varied. In general, nocturnal forms or fishes living deep to the surface of the water have mainly rods in the retina; diurnal or surface forms may have a good percentage of cones, but in general cones are relatively rare and color sensitivity is probably as high as our own in relatively few vertebrates. Rods and cones may be present in any retinal region, but cones when present are commonly concentrated (as in ourselves) in an area centralist at the back of the retina.

Inward from the rods and cones is a layer of bipolar cells, with processes which, on the one hand, pick up impulses from the rods and cones and, on the other, transmit them inward to the third layer, that of the ganglion cells which form the optic nerve. It appears that often one cone cell alone connects with a given bipolar cell, and only one such bipolar cell connects with an associated ganglion cell; thus each cone may have an individual pathway to optic nerve and brain. In contrast, a considerable number of rods converge into a single bipolar

cell; in consequence, the brain obtains no information as to which of the group of rods has been stimulated, a condition which accounts for the lack of precision in rod vision as compared with that of cone areas.

Optic Norre. Although violating proper order (since the nervous system is the subject of the next chapter) we may permit ourselves to discuss the central connections of the eye in relation to vision. The ganglion cells, situated on the inner surface of the retina, produce long fibers which converge to a point near the center of the retina, plunge through it (with the production of a "blind spot" because of absence here of rods and cones) and travel along the eye stalk to the brain as the optic nerve. While this is customarily called a nerve, it must be pointed out, that since the retina is, from an embryologic point of view, properly a part of the brain itself, the optic nerve is to be thought of not as a true, external nerve, but rather as a fiber tract connecting two brain regions.

As they reach the floor of the forebrain, the two optic nerves form the Xshaped optic chiusan (Fig. 345); in this crossroads, in most vertebrates, next all the fibers of the right optic nerve cross to the left side of the brain and vice versa; such a crossing of fibers is termed a decussation. In most vertebrate classes the two sets of fibers continue upward and backward to brain centers in the roof of the midbrain (tectum); in mammals almost all the fibers are, instead, relayed to a pair of special areas in the gray matter of the hemispheres.

In a majority of vertebrates the eyes are directed laterally, with nearly disincet fields of vision on either side, and the brain builds up two separate pictures of two separate views. In a number of higher types, however—such as birds of prey and many mammals—the eyes are turned forward, the two visual fields over lap, and the two sets of impressions transmitted to the brain are more of reseable. In such cases the formation of two duplicate mental pictures seems an unnecessary procedure. Nevertheless this is done, as far as can be discovered, in nommammalian forms, no matter how much overlap exists.

In many mammals, however, there appears stereoscopic vision; the two fields are mentally superimposed, with the result that such a form as man is aided, by the slight differences in point of view of the two eyes, in gaining effects of depth and three dimensional shape of objects which are otherwise impossible of attainment. Associated with this new development is incomplete decusation at the chi-asma. In mammals—and in mammals alone—we find that for those parts of the field which overlap, fibers from the areas in both retinas which view the same objects go to the same side of the brain. In consequence, certain groups of fibers

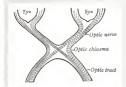


Fig. 345. Diagram of the optic chiasma in a mammal with good stereoscopic vision. All fibers from the corresponding half of each eye pass to the same side of the brain. (From Arey.)

do not cross (i.e., decussate), but turn a right angle at the chiasma to accompany their mates from the opposite eye. In man, for example, where the overlap of visual fields is nearly complete, practically all fibers from the left halves of both retinae enter the left side of the brain and those from the right halves enter the right side (Fig. 345). As a result, the visual area of each brain hemisphere builds up a half-picture of the total visual field as a "double exposure"; by further complicated interconnections between the hemispheres, the two halves of the picture are welded together to emerge into consciousness as a single stereoscopic view.

Accessory Structures. We have earlier described the series of striated muscles which move the eyeball. Other external structures have to do chiefly with protection and care of the eye's external surface. Except in some sharks there is little development of eyelids in fishes. Lids are, however, developed in some fashion or other in all tetrapods, a dry cornea would become opaque, and closing the lids at intervals moistens and cleans the corneal surface. Upper and lower lids are always present and generally are opaque. In most groups the lower lid is the more prominent, but in mammals (and crocodilians) the reverse is true. In replies and birds generally and in many mammals there is a third eyelid, the nictivating membrane, a transparent fold of skin lying deep to the eyelids and drawn over the cornea from the anterior (or medially to obserior marsins.

No muscles were originally present in the eyelid region, and various mechanisms have been evolved to move the lids. In some instances in lower tetrapods their movement is a passive one, opening and closing as the eyeball is pushed out or withdrawn; in other cases slips from the eyeball muscles extend forward to operate the eyelids. In mammals the facial muscles, grown forward over the head, form a ring of fibers which operate as a sphincter muscle in closing the eye (Fig. 1944, p. 221).

In land vertebrates are developed lacrimal glands, furnishing a "salt solution" to moisten the cornea. In such primitive forms as the urodeles there is a row of small glands along the inside of the lower lid; in anurans, reptiles and birds there tends to be a concentration of gland development at the front (or medial) margin of the orbit; in mammals the lacrimal gland is usually developed at the outer or back corner of the eye. A useful adjunct, present in all tetrapods (except in turtles, where it is secondarily lost) is the tear duct (lacrimal duct), carrying surplus fluid from the corner of the eye to the nasad cavity.

Median Eyes. Ancestral vertebrates had a third eye, medially situated on the forehead and directed upward. In the oldest ostracoderms (as in Fig. 19, A, p. 38) a socket which obviously contained such an eye is universally present and often conspicuous, although always much smaller than that of the paired eyes. This eye was generally present in the placoderms and present in Devonian bony fishes of all major groups. Further, it was universal in all the older land vertebrates---ancient amphibians and Paleozoic reptiles of all sorts. By Triassic times, however, this accessory visual organ appears to have gone out of fashion. Today, median eyes are present only in lampreys, on the one hand, and Sphenodon and some lizards on the other (Fig. 393, p. 396); buried under the skin, they can do little more than detect the presence or absence of light, although a miniature cornea, lens and retina may be developed. Like lateral eyes, these median eyes are brain outgrowths. There is, however, a curious complication in the story: the median eye, it appears, is not the same throughout, but may develop from either of two dorsal outpocketings of the brain roof, the parietal organ (parapineal organ) and pineal organ. Both develop eye structures in the lamprey; the former

only in lizards and Sphenodon. The situation suggests that possibly the remote ancestor of the vertebrates may have had paired dorsal eyes as well as paired lateral ones. Despite loss of function, the pineal organ persists in higher vertebrates as a seemingly glandular structure of uncertain function.

# LATERAL LINE ORGANS

A highly developed sensory system of a type quite unknown in land dwellers is that of the lateral line organs (Figs. 346, 347) found in fishes and aquatic larval amphibians. The receptors are sensory cell clusters, the neuromasts, described below; these are generally situated along a series of canals or grooves on the head and body. A main element of the system is the lateral line in the narrower sense of the term—a long canal running the length of the trunk and tail. It continues forward onto the head, where similar canals form a complex pattern, typically including branches running forward both above and below the orbits and downward to run forward along the lower jaw. Isolated neuromasts, termed pit organs, may also be found on the head of fishes, and in modern amphibians the arrangement of the neuromasts on the head is discontinuous, with little evidence of linear arrangement. The canals in which the sensory organs are generally enclosed open to the surface at intervals by small pores; in a few fishes open grooves take the place of canals.

The sense organs of the lateral line system are the neuromasts, consisting of bundles of cells which have much the appearance of taste buds. Each elongate sensory cell has a hairlike projection; invariably present above the "hairs" and enclosing their tips is a flexible mass of gelatinous material secreted by the neuromast cells, which may be termed a capula (Fig. 348). The neuromast organs are innervated by cranial nerves—most of those on the head by nerve VII, the entire body line by nerve X.

As we lack structures at all comparable to these ourselves (except, as we shall see, in the internal ear), the nature of the sensations registered by them has been difficult for us to determine. It appears that they respond, by movement of the cupula and consequent bending of the "hairs," to water vibrations or currents and thus aid the fish in locomotion through the water, where visible "landmarks" are seldom present. Many reptiles and mammals have returned to an aquatic existence, but this useful sensory aid, once lost, never reappear.



Fig. 346. Section through the skin of a teleost, to show the lateral line canal, ke, piercing a series of scales, and opening at intervals to the surface, and opening at intervals to the surface, which sends branches to the sensory organs, so; ep. epithelium. (After Goodrich.)

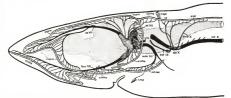


Fig. 347. Left side of the head of a shark to show the lateral line canals (parallel lines) and the nerves (black) supplying them. Pit organs are not shown the VII, baccal ramss of nerve VII; chand, hyemandibus lar canal; enfo; infraorbital canal; clat, lateral line canal proper; end, mandibast canal; cope, supnorbital canal; copi, supratemporal (or occipital) onails; et. temporal canal; don X, donsal ramss of nerve Xi at X, lateral line ramss of nerve. Num VII, step anashibush ramss of nerve VII; or VII, superlicial ophthalmic ramss of nerve VII; or VII, otic ramss of nerve VII; por IX, supratemporal ramss of nerve X; pox X, supertaineporal ramss of nerve. V, (Form Norris and Bughes.)

## THE EAR

First thoughts as to the primary anatomic or functional aspects of the vertebrate ear are liable to be misleading when based on familiar human features. One tends to think, when the word is mentioned, of the ornamental pinns of the mammalian ear, or, perhaps, of the middle ear cavity behind the drum, with its contained ear ossicles. These items, however, are entirely lacking in fishes; the basic ear structures of all vertebrates are those of the internal ear, the sensory structures buried deep within the ear capsule. We naturally think of hearing as the proper ear function. But in the ancestral vertebrates audition was apparently unimportant and perhaps absent; equilibrium was the primary sensory attribute of the "auditory" oran.

The Ear as an Organ of Equilibrium. Before considering the hearing function, which becomes increasingly important as we ascend the vertebrate scale, we may discuss the ear as an organ of equilibrium, a basic function which remains relatively unchanged from fish to man. Equilibrium is a type of sensation produced by the internal ear alone; all accessory ear structures are related to hearing and need not concern us at the moment.

In a variety of fishes, amphibians and reptiles the paired internal ears are built upon a relatively uniform pattern in which most of the structures present are relatived to equilibration (Fig. 349, A-D). The membranous labyrinth consists of a series of closed sacs and canals lying within the ear capsules on either side of the braincase and containing a liquid, the endolymph, not dissimilar to that of the interstitial spaces. Ivo distinct major saclike structures are generally present, the attriculus above and, more ventrally, the sacculas. A slender tube, the endolymphatic duct, usually extends upward and inward from them to terminate within the braincase in an endolymphatic sac. In both major car vesicles there is found a large oval "spot" consisting of a sensory epithelium associated with branches of the auditory nerve; these are the utricular macula and the saccular macula. A 358 THE VERTEBRATE BODY



Fig. 348. Neuromast sensory organs. Left, an organ from a lateral line canal: right, the crista from a semicircular canal. In both are seen supporting cells and sensory cells, the latter with hairlike processes extending into the flexible, gelatinous cupula. (Partly after Fulton.)

pocket-like depression is formed in the floor of the sacculus. This is the lagena, which contains a small lagenar macula. The sensory cells of these meaules (and, indeed, of the entire internal ear) are comparable to the neuromast cells of the lateral line system, having hairlike projections embedded in an overlying gelationsus material. In the utricular and seccular meaules, and often that of the lagena as well, this material becomes a thickened structure in which are deposited crystals of calcium carbonate, forming an "carstone," an otolait, (in any inned fishes the otoliths are massive structures which may fill almost the entire cavity of the two vesicles.)

The utricular macula, and to a much lesser degree, those of the sacculus and lagena, register, by the tilt of the otolith and bending of its sensory "hairs," the position of the head and linear acceleration; somewhat similar organs are found in a number of invertebrate types. They do not, however, furnish information as to turning movements. This is the function of another series of organs, the semicircular canals.

These tiny tubes spring out from the utriculus and connect with it at either a line of the property and the present and outward from the upper surface of the utriculus, and the posterior retircal canal, running backward and outward; a horizontal canal extends laterally. Each canal has at one end a spherical expansion, an ampulla. The vertical canals bear these at their outer and lower ends, anteriorly and posteriorly; the horizontal canal (for no known reason in particular) has its ampulla anteriorly placed. Within each an expulla is a sensory area, usually elevated, termed a crista (Fig. 348). Here we find again the familiar neuromast "hair" cells, their tips embedded in a cupula. It seems clear that their function is to register turning movements in the several planes of space; displacement of liquid in one or more canals displaces the cupulae, with consequent hending of their sensory hairs.

Despite the fact that these organs of equilibrium are essentially uniform in

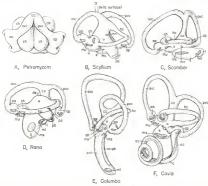


Fig. 349. Membranous labyrinth of Λ, lamprey; B, shark; C, ledoots D, frog; E, kird, E, mammak all external views of the left ext. Sensory areas ner-home (except in A) as if the membrane were transmit, on, Ampulla of anterior canak, δ, ampulla of posterior canak; and, ampulla of posterior canak; and, ampulla of posterior canak; and, anterior vertical canal; c, cocloler sdur; c, c, reasonmouse with which both vertical canals; c, canals; one cat, define the lamprey car lined with a ciliated epithelium; δ, endodymphatic date; δc. horizontal canal; ℓ, lagens; and, meantle of lagens; no, macula of lagens; no, macula of lagens; no, macula of nativelus; no, macula nativelu

basic structure in every jawed vertebrate, some variations occur here and there. For example, in sharks, sacculus and utriculus form but two parts of a common sac; in rays the canals are connected only by narrow ducts with the remainder of the system. The endolymphatic duct usually terminates in a sac of modest size within the brain cavity but in frogs may expand the length of the cavity of the spinal cord, and in sharks the duct extends upward to open on the top of the head. The most unusual conditions are found (as in other organ systems) in the cyclostomes. The lamprey has but two semicircular canals; the hagfish but one. As in the case of the nose, we cannot be sure whether the cyclostome condition is a primitive or a degenerate one.

Origin of the Vertebrate Ear. Embryologically, the internal ears first appear, like the lateral line organs, as ectodermal thickenings on either side of the head (Fig. 350). These sink inward to form a pair of sacs, which for some time may retain a connection with the exterior (as do the endolymphatic ducts in an adult shark). Typically, each sac then divides into utricular and saccular portions; from the former there separate off the semicircular canals, and from the latter arise further structures, discussed later.

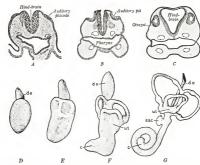


Fig. 350. Diagrams to show the development of the internal ear in mammals. 4 to C. Cross sections of the head of early embryous an ectodermal placede sinks inward on either side to form an otic vesicle. Do to C. Successive stages in the development of the various parts of the membranous labyrumli from the otevenicle, c, oxchicar duct; de, endolymphatic duct; soc, sacculus; at, utriculus. (A to C from Arcy; D to F stafer His and Bremers.)

This embryologic story, together with the nature of the sensory endings of the ear—which closely resemble the externally placed neuromast organs—suggest that the internal ear originated phylogenetically as a specialized, deeply sunk part of the lateral line system. As will be noted in the next chapter, the nerves from the two sets of organs are closely associated. The two are closely associated functionally as well, furnishing a fish the major part of the data by which its locomotion is regulated.

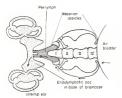


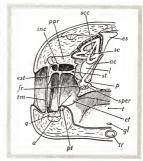
Fig. 35.1. Diagrammatic horizontal section of the posterior part of the head and anticric part of the body of a teleost with weberian ossicles. Vibrations in an anticrior subdivision of the air bladders et up corresponding vibrations in a series of small ossicles which in turn set up waves in a perlayuplatic sac at the base of the three personal personal production of the production of the vibrations. Some numerals indicate the vertexer from which the weberian ossicles are derived. (After Chvanilov.)

Hearing in Fishes. Although not the primary function of the internal ear, hearing is certainly present in many fishes, particularly among the teleosts, but it is uncertain as to which one or more of several sensory maculae are concerned. The saccular macula may be the main receptor in most cases, but possibly the lagenar and main utricular maculae may be involved and another possible suspect is the macula neglecta (Fig. 349, B, C), a small sensory spot in the utriculus of many fishes and lower land vertebrates.

Although fishes lack the middle ear apparatus utilized by land vertebrates in bringing external vibrations into functional relations with the sensory areas in the internal ear, several groups of teleosts have independently evolved comparable structures. Thus, a group including the catfishes, minnows and carp (Ostario-physii) use the air biadder as a resonating chamber and carry vibrations forward to the ear by a series of small bones, termed the weberian ossicles, derived from the anterior vertebrae and ribs (Fig. 351).

The Middle and External Ear in Amniotes. Hearing is an important sense in tetrapods, but the sounds to be heard are relatively faint air waves which can ordinarily have little direct effect in setting up endolymph vibrations in the internal ear. Devices for amplification of these waves and their transmission to the internal ear are ancessity. Such devices, established, it seems, in very early tetrapods, are retained with little change in such reptiles as lizards (Figs. 352, 353, 4–C). The spiracular gill cleft and the hyomandibilar hone are the elements utilized. The spiracular pouch of the embryo never breaks through to the surface. The corresponding surface depression, where developed, is an external auditory meatus; the thin membrane between this depression and the pouch becomes a middle ear cavity; its connection with the throat is the eutschian tube. The fish hyomandibular hone changes its function to become a rollike stapes (or columella); this crosses the middle ear cavity from the drum

Fig. 352. Posterior view of the left side of a lizard head to show the auditory apparatus. A shallow external depression leads to the ear drum (tm). Internal to the drum, the stapes is seen, divided into two parts. the "extracolumella" (est), and columella or stapes proper (st); processes from the former articulate above with the skull (inc) and below with the quadrate anterior to the middle ear cavity. This cavity opens by a broad eustachian tube (et) to the throat. The internal ear is shown in diagrammatic fashion. Other abbreviations: a, articular bone of lower jaw (= malleus); ac, inner wall of auditory capsule; es, endolymphatic sac; fr, fenestra rotunda; gl, glottis; l, lagena; p, perilymphatic duct connecting inner ear with brain cavity; ppr, paroccipital process of otic region; pt. pterygoid; q, quadrate (= incus); sc, sacculus; scc, semicircular canals; sper, position of perilymphatic sac; t, tongue; tr, trachea. (From Goodrich, after Versluys.)



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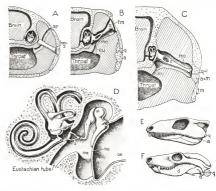


Fig. 3.53. Diagram to show the evolution of the middle car and auditory ossieles. Diagrammate serious frough the other repolar discharge of the active repolar forms frough the other repolar forms from the manual (showing the car region only); E. side view of the skull of a primitive ambibilities. Ca primitive repolar Da a turnamal (showing the car region only); E. side view of the skull of a primitive land vertebrate. For a mammal-like repuls to show the shift of the carbon from the on noted to the skull to the region land to the shift of the region from the carbon from the one of the shift of the region of the shift of the shif

to an opening through the otic capsule into the internal ear, the fenestra oralis. It thus transmits vibrations picked up by the drum to the liquids of the internal ear and, eventually, to its contained sensory structures. The availability of the hyomandibular for its new function was due, as discussed in an earlier chapter, to its being no longer required for jaw support; it may, however, retain a process connecting with the quadrate region of the jaw articulation. As in the lizard condition of Figure 352, the stapes may form in two or more pieces and develop still further processes connecting with the skull or hyoid arch. The bird middle ear is similar to that of reptiles.

In mammals, external ear structures become prominent for the first time. There is a deep, tubular external meatus, and there is almost always a projecting pinna which may be of value as a collector of sound waves. A more fundamental change, however, is that seen within the middle car cavity (Fig. 553, D). Here, instead of a single bone, there is present an articulated series of three auditory ossicles leading from eardrum to oval window—malleus, incus and stapes (hammer, anvil and stirrup). The origin of this series of ossicles was long debated. It was thought at one time that they might be due to a subdivision of the single

reptilian element. Embryology, comparative anatomy and paleoatology combined have, however, revealed the true story. The inner element, the stapes, although much shortened, is equivalent to the whole stapedial apparatus of reptiles. The other two elements are homologous with the articular and quadrate hones which in lower vertebrates form the jaw joint. Manmals have evolved a new joint system for the jaw; the older joint structures have been put to new use. The reptilian eardrum lay close to the jaw joint: the articular has remained attached to it and become the malleus. The quadrate, connecting with the articular, on the one hand, and the stapes (the old fish hyomandibular) on the other, retains these connections as the incus. These bones, originally still bar elements, afford a good example of the changes of function which homologous structures can undergo. Breathing aids have become feeding aids and, finally, hearing aids.

The Internal Ear in Reptiles (Figs. 354, 355, B; 356, A). In tetrapods the parts of the internal car devoted to equilibrium show little change; the auditory apparatus, however, gradually develops into structures which attain such size and importance that the older regions of the sacs and canals are often termed (rather slightlingly) the resulbule of the internal ear.

It is the lagenar region in which this expansion takes place. The macula of the lagena persists in tetrapods, except in mammals above the monotreme level, but is unimportant. A second sensory area developed here—the basilar papilla is the auditory organ of tetrapods, to which vibrations, brought in from without by the stapes, are received.

Between the walls of the ear capsule and the sacs and canals of the endo-

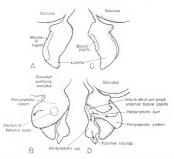


Fig. 35.1. The car of a late embryo of a litted (Lacerta), A, Left ear, lateral view of the membranous laberinth in the floor of the sacculus and the lagera. B. The same with the perilymphatic system shown in addition. C. D. Medial views comparable to A and B, respectively. Arrows indicate course of conduction of vibrations from stapes to hashir papilla and on to the "round window" at the distal end, beyond the perilymphatic dart.

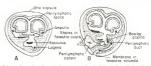


Fig. 355. A. Schematic section through the car capsule of a fish, to show the perilymphatic space surrounding the membranous labyrinth containing endolymph. B. Similar scheme of a tertapod, in which a part of the perilymph area (arrows) is specialized to conduct sound from the fenestra ovalis to and past the auditory sensory area. The maculus are darkly shaded, (Afred 6e Burlet.)

lymph system are spaces crossed by connective tissue strands and filled by a second ear fluid, the perilymph (Fig. 355). In tetrapods there is organized in the perilymph a conduction system which forms the last link in the transmission of vibrations to the basilar papilla. The stapes brings vibrations to the oval window. Inside this there is developed a large perilymphatic cistem, against which the stapes plays (Figs. 354, 355, B; 356, A). Vibrations received here are carried in a perilymph-filled duct around the lagena to its posterior border. At this point the duct lies beneath the basilar papilla and is separated from the under surface of its sensory cells only by an elastic basilar membrane. Vibrations of this membrane agitate the hair cells in the papilla, and at long last, in this roundabout fashion, the sensory organ is reached. This situation—an auditory sensory structure agitated by vibrations of the membrane at its base—is a fundamental feature in the construction of the apparatus in all amniotes. We shall find it repeated, and capable of description in much the same words, in birds and mammals.

As a final point here, it must be noted that a release mechanism for the vibrations carried must, of course, be set up at the far end of the perilymph duct.

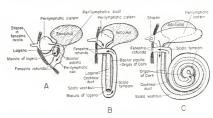


Fig. 35.6. Diagrammatic sections through the saccular region to show the evolution of the coeblea. A Primitive reptile with a small basidar papilla adjacent to the perhymphatic duct. B. The crocodile or hird type; the lagera has elongated to form a coeblear duct, the basilar sense organ with it, and a loop of the perhymphatic duct follows the coeblear duct in its elongation. C. The mammalian type; the coebles is further elongated and coile in a fashion consomized of space.

This mechanism was primitively a perifymphatic sac, projecting into the braincase. In most tetrapods, however, there is a further development. A "round win-dow"—the fenestra rotanda—develops in the walls of the otic capsule, facing the middle car cavity; a membrane here vibrates in phase with the impulses received through the oval window at the other end of the perifymph system.

Development of the Cochlea (Fig. 356). Both birds and mammals have greatly refined their hearing ability by the development of a cochlea. The crocodilians demonstrate the manner of its development. Three structures are involved—the lagena, the perilymphatic duct and the basilar papilla, The lagena expands into a long tube, filled of course with endolymph; this is the cochlear duct for scala media). The basilar papilla is likewise expanded into an elongate structure, running the length of the cochlear duct, as the organ of Corti. The perilymphatic duct, clongating beneath it in corresponding fashion, becomes a double loop. The part of the loop leading in from the oval window (in the vestibular part of the car) is termed the scala vestibular; the distal limb, leading to the round window (which is covered by a "tympanum") is the scala tympani. The three tubes—the endolymph-filled cochlear duct and the two perilymph-filled scalae—are closely pressed together and form a primitive cochler.

The bird cochlea differs from that of a crocodilian mainly in greater elongation of the structure. In mammals there is still further lengthening of this triple tube system, as its name implies, it is in mammals coiled into a tidy spiral to keep it within the bounds of the ear capsule.

We cannot here discuss in detail the complicated microscopic structure of the organ of Corti (Figs. 357, 358) which includes a complex system of sensory and supporting cell types and a covering membranous flap. An important element is the basilar membrane which underlies the organ. As in lower tetrapots, vibrations of this membrane by waves brought in by the perilymph system are

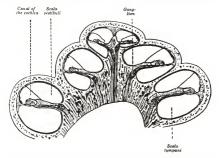


Fig. 357. Diagrammatic section through a mammalian cochlea. (After Finnerty and Cowdry.)

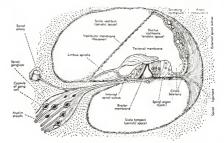


Fig. 358. A much enlarged section through a mammalian cochlea to show details of the organ of Corti (cf. Fig. 357). (From Ruch and Fulton, Medical Physiology and Biophysics.)

responsible for stimulation of the organ of Corti. The functional "reason" for elongation of the hasilar papilla appears to be discrimination of sounds of different pitch; the membrane grades in width along its length and is, in correlation, sensitive to different wave lengths at different parts of its extent.

The Ear in Amphibians. We have above omitted any reference to ear construction in living amphibians for the reason that conditions in these forms are not, in general, primitive but specialized and seemingly degenerate in most cases and are, further, extremely varied. Four main points may be noted: (1) The drum and middle ear cavity are often missing; (2) the stapes is frequently reduced or absent; (3) a second ossicle, the operculum, is frequently present in the

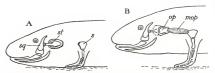
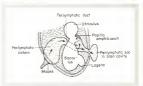


Fig. 359. Diagram to show mechanism of communication between exterior and inner ear in modeles. A. An aquatic form in which the stapes, or columella, picks up vibrations by a ligamentous attachment to the squamousl. B. At type in which the stapes is reduced, and the operculum picks up ground vibrations through a muscular connection with the shoulder griftle, map, Opercular muscle; up, operculum; v scapulic up, squamousl', at stapes. (Merc Ringsbury and Reod).

Fig. 360. Schematic section of the internal car in a salamander. The basilar papilla is absent here, but is found in addition to the papilla amphibiorum in anurans. (After de Burlet.)



open window; (4) the basilar papilla is often absent and a special amphibian papilla functions in its stead.

Many frogs have an eardrum and a well-developed stapes, but drum and middle ear cavity are absent in some anurans and in all members of the other two orders, and such hearing as is possible in these forms must be accomplished by using other types of "pickup," such as the two shown in Figure 359. The operaculam is a flat plate, apparently a detached segment of the wall of the capsule, which lits into the oval window in company with the stapes or, in urodeles in which the stapes is lost, occupies the entire oval window. In the internal ear (Fig. 360) frogs retain the basilar papilla, but this is absent in urodeles, and in both cases there is present a special sensory area, the papilla amphibiorum, which appears to play the main role in hearing in this class of vertherates. Evidently, auditory structures were in an experimental stage in the ancestral tetrapods. As in many other features, the ancestors of the modern amphibians chose a series of less progressive paths in ear evolution than did those among their ancient relatives who gave rise to the aminites.

# 16

# THE NERVOUS SYSTEM

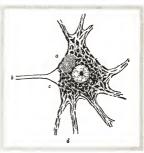
In a protozoan the single cell in itself receives sensations and responds to them. In higher, metazoan organisms there tends to be, to an increasing degree, a differentiation between cells specialized for the reception of sensations—receptors—and those which make the appropriate response—the effectors. In lowly forms the relations between these two types of cells may remain relatively simple; receptor cells may, by their physical and chemical activities, arouse their neighbors to respond. Even in vertebrates there is a retention of such a primitive method of stimulation in the circulation of hormones. But in most metazoans a means for more direct, rapid and specific transmission of stimuli is present as the nervous system.

In primitive metazoans, such as coelenterates, this system may be merely a diffuse network of cells and fibers preead through the tissues. But in most animals of any degree of complexity the nervous system is more highly organized, with nerve trunks and centers where transfer of impulses between fibers takes place. In most groups a dominant center, a brain of some sort, makes its appearance. In the vertebrates the brain is situated anteriorly, close to the major sense organs, with a single dorsal hollow nerve cord—the spinal cord—running backward from this along the body. Brain and cord form the central nervous system. Running outward are numerous paired nerves, along which ganglia—clusters of nerve cells—may be found; these nerves and ganglia constitute the peripheral nervous system.

# STRUCTURAL ELEMENTS

The Neuron. The nervous system contains numerous cell bodies, but more prominent are bundles of sleared but elongate fibers which make up much of the bulk of the system. It was once thought that the fibers and cell bodies were independent of one another; it presently became clear, however, that this is not the case, and that the fibers are, universally, processes of cells rather than inde-368 THE NERVOUS SYSTEM 369

Fig. 361. The cell body of a motor neuron from the spinal cord of an ce, a, a mass of pigment. At b is the axon, with a clear cytoplasmic area the "axon Billock", c, at the base; the remaining processes, d, are dendrites. Much of the the cytoplasm is filled with readily stainable but masses of material, the Nisal bodies. The large material than the complex of the contraction of the contraction nucleus contains a prominent cluster of chromatin, the nucleolus. (From Herrick, after von Lenhossek).



pendent structures. The basic units of the nervous system are neurons; each consists of a cell body and its processes, long or short.

Most of the cell bodies of the neurons are situated within the central nervous system. The shape is frequently stellate, because of the presence of multiple processes; with appropriate stains, microscopic preparations show in the protoplasm various characteristic structures, such as are illustrated in Figure 361. Most notable are Nissl bodies, containing large amounts of the nucleic acid RNA; this indicates that the cell body is the "manufacturing center" for the whole neuron, and the materials formed here flow out into the axon and other processes. In the adult there is very little evidence of cell division in the neurons, indicating, as a peculiarity of the nervous system, that a full complement of nerve cells has been attained by about the time of birth or hatching. In consequence (although cell processes may regenerate), destruction of a nerve cell through injury or disease is a nermanent loss.

Nerve Fibers. Extending outward from the cell body of the neuron are slender processes, whose distribution and lengths are quite variable. Most often thought of as typical are such neurons as those that innervate striated body muscles (Fig. 362, 4). In these motor neurons short processes, slender, numerous, and branching, carry impulses inward toward the cell body; they are termed dendrites, from their treelike appearance. There is a single axon, a relatively stout and elongate process, which may be in large animals as much as several yards in length, carrying impulses away from the region of the cell body. A second common type is that of the afferent neurons that carry sensory stimuli inward to the central nervous system (Fig. 362, B); here the long process leading in from the point of reception to the cell body adjacent to the cord, as well as a second long process, which enters the cord, are comparable in structure to the axon of a motor neuron.

Functionally, the most important part of a major nerve fiber is its central structure, the axis cylinder, a strand of protoplasm continuous with that of the

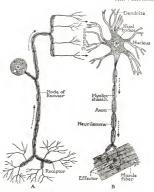


Fig. 362. Two types of nerve cells, A. Alterent (sensory) neuron of spinal and cranial nerves: long axon-like processes run from sensory receptor to cell body in spinal ganglion and thence into cond, where ramification occurs. B. Efferent (motor) neuron, with vell body in croal and a long axon (labbravated in the figure) extending out to the effector (muscle thee). (From Millard, King and Showers, Human Anatomy and Physiology.)

cell body. Its appearance is homogeneous in unstained materials; however, appropriate stains or study under the electron microscope show the presence within it of numerous threadlike, longitudinal neurofibrils. Cyclostomes apart, all fibers except the very smallest, central or peripheral, are covered by a myelin sheath of fatty material. When the sheath is well formed, it gives a shiny, glistening appearance to the fibers. In some cases (as the postganglionic fibers of the autonomic system, described later) the sheath is thin, or a single sheath may be spread out to cover a series of small fibers. In such instances the sheath ordinarily is not observed and hence (incorrectly) assumed to be absent. In the case of fibers within the spinal cord or brain, a continuous sheath is laid down by adjacent, supporting, cellular elements. In peripheral fibers, the sheath is formed by special sheath cells (Schwann cells), which wrap themselves around segments of the axis cylinder in a fashion crudely comparable to a jelly roll (except that the "rolls" are very numerous and very thin). In the intervals between the territory of two successive Schwann cells, the myelin sheath of peripheral fibers is interrupted and there is found a node of Ranvier. In fibers outside the central nervous system, there is a further and continuous covering, a tough, inelastic membrane, the neurilemma, also produced by the sheath cells.

If a fiber is cut, the portion distal to the cut degenerates and the proximal

region and cell body may show evidence of damage. Peripheral fibers frequently regenerate, growing out from the stump connected with the cell body; they are aided, it seems, in seeking out their former paths by persistence of the sheath cells which surrounded the former axis cylinder. Experimental cutting of fiber bundles in the brain or cord may be of aid, through differential staining of degenerating fibers, in the difficult task of determining the complicated "wiring" structure of the nervous system.

By analogy one tends to compare nerve transmission with an electric impulse, and it can be demonstrated that as a nerve impulse travels along a fiber there is a momentary change of the electric potential at the fiber surface, a "ripple of leakiness" traveling along the membrane. Rapid metabolic changes occur simultaneously in the axis cylinder—changes analogous to those in muscle contraction, making for rapid release of energy. However, a nerve impulse, though rapid, cannot be compared for speed with electricity. Even in the speediest mammalian fibers the rate is only about 100 yards per second; in lower groups the rates are on the average considerably slower. It is obvious that in the case of large animals (such as an elephant) the time lag between reception of a stimulus and reaction to it, even by the simplest reflex, may make coordination difficult.

The major qualities of nerve impulses may be briefly noted. An impulse is anonymous and nonspecific. The nature of a semation "felt" in the brain depends upon the centers which receive it, not in any difference in the type of impulse received, could the "wiring" be changed, nerve impulses from the nose, for example, would give a sound effect if received in an auditory center. A nerve filter is quite capable of transmitting an impulse in either direction. The undirectional transmission normally found is due to the pattern of fiber connections; neurons are anatomically "polarized." As in the case of contraction of a musele fiber, a nerve impulse is an "all or none" phenomenon. However, the strength of impulses along nerves as a whole may vary. There may be differences in the number of individual fibers stimulated; further, impulses do not ordinarily come singly, and a rapid sequence of impulses may (we noted earlier) have a cumulative effect on a muscle fiber, of example.

The Synapse. Never does a single neuron span the entire distance between the sensor preceptor initiating an impulse and the muscle or gland stimulated; action takes place through a chain of neurons, always two and usually more. The point of transfer between successive neurons is termed a synapse. Typically the tip of an axon breaks up into fine fibrils which lie close to the dendrites or cell body of the second neuron, but do not come into actual contact. The timing of nerve transmission shows that a distinct interval of a tiny fraction of a second is taken in bridging the gap at a synapse. There are rival theories as to the method by which the synapse is crossed. One belief is that it is electrical, a "spark" bridging the gap; the other, now more generally accepted, that it is chemical, the fibrils giving off minute amounts of a substance—usually acetylchic—which stimulates the next fiber. In some peripheral situations it is definitely known that such chemical materials—neurohumors—are actually given off; the situation is less clear in the central nervous system.

The Reflex Arc (Figs. 363, 364, A). Before considering more complex structures, we may note the general nature of the simple type of nerve action known as a reflex, seen in such situations as the "automatic" withdrawal of a bare foot that has trod on a tack or of a finger that has touched a hot stove. A sensory stimulas picked up from receptor cells or fibril tips is carried toward the central nerv-

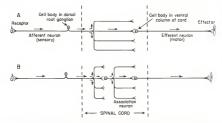


Fig. 363. Diagrams to show simple reflexes. Area between broken lines is part of arc lying within the cord (cf. Fig. 364). A, Two-neuron reflex; B, association neuron interpolated, increasing the number of possible paths.

ous system by a long afferent or sensory nerve fiber. The cell body of the sensory neuron to which such a fiber belongs lies in a ganglion close to cord or brain, but the fiber continues directly past it into the central nervous system. Here it normally branches to synapse with and potentially stimulate a whole series of neurons. Conversely, each of these neurons may receive impulses from numerous afferent fibers, so that a considerable amount of interplay between receptors and effectors may take place.

In the simplest of reflexes the neurons here stimulated may be efferent usually motor neurons, whose cell bodies lie in the cord or brain and whose long axons run out to effector organs (usually muscle fibers). But even a simple reflex is generally one stage more complicated and is a three-neuron chain. Afferent fibers usually do not synapse directly with motor cells but with association neurons contained entirely within the central nervous system; these, like the affer-

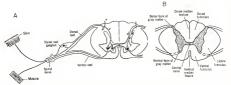


Fig. 364. A. Diagram of mammalian spinal cord and nerve to show path of reflex arc. A sensory fider entering by the dorsal root may send branches, a, b, up and down the cord. At various levels the sensory fiber may connect with motor neurons of the same side, c, or opposite side of the cord, d; or with association neurons, c, B, Diagrammatic section of a mammalian spinal cord, to show distribution of white and gray matter and funcial: (After Gardner;)

ents, send out branching processes which connect with numerous motor cells. This further multiplies the number of possible responses to a sensory impulse and, conversely, the number of sensory impulses which may produce a given motor effect. Quite surely no single afferent impulse is sufficient to activate an efferent neuron; the action is caused by a summation of stimuli received, giving rise to phenomena of "choice." We have here clues as to the way in which brain mechanisms more complicated than these simple reflexes may have been built up—namely through the development of higher association centers, with the interpolation of further series of association neurons, into which a wide variety of sensory impressions may drain and from which may come a wide variety of responses.

## SPINAL NERVES

In general the peripheral nervous system is simply constructed. It consists essentially of the nerves which penetrate to almost every region of the body—groups of nerve fibers, sheathed by connective tissues, carrying afferent impulses from sensory endings to cord and brain and carrying outward efferent stimuli to muscles and glands. It includes, as well, the ganglia, found along the course of nerves, which contain cell bodies of sensory neurons.

Typical paired spinal nerves (Figs. 364, Å, 365) are generally present in every body segment. There are two roots. The ventural root runs straight outward from the ventral margin of the side wall of the cord; the dorsal root, bearing a prominent ganglion, enters the cord higher up the side wall. In most vertebrates the two roots join to form a main trunk, from which various branches—rami—diverge. Neglecting for the time a ramus running toward the viscera, there is usually a dorsal ramus to the muscles and skin of the back and a ventral ramus

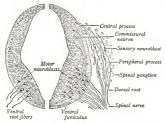


Fig. 46.5. Sections of the spinal cord of early mammalian embryos. Left, axons are growing outward from motor nerve cells. Right, association or commissiant neurons are developing within the orde sensory neurons are developing externally from neural rest cells (Fig. 64, p. 101). These sensory neuroblasts are at this stage lipolar, i.e., with separate proximal and distal processes; later the two processes have proximally in higher vertebrates to give a unipoiar condition to the mature aggingion cell. (From Arcy)



Fig. 366. Left, serve picture supplying the left pelvic fin of a chimaera, showing interchange of their bundles between members of the series of spinal nerves concerned. The two rects and the dorsal guplis of the nerves concerned are shown at the top of the figure; the base of the fin is at the bottom. Right, on a larger scale, the hearbid pickurs supplying the pectors limb of an arman, The rever vero tax of shown, and the hearbids when the pickurs are cut short of their terminations, the largest trank is that of the radial nerve supplying than the the attrict of the slevius is comblex. (But the group, carried when Wingster of the slevius is commissed, the larges trank is that of the radial nerve supplying this, but the attrict of the slevius is commissed.

to the more lateral and ventral parts of the body wall. The nerve trunk and its major branches carry both afferent and efferent fibers; the two roots, however, show a sharp division of functions. The ventral roots carry efferent, motor fibers whose cell bodies lie within the cord (Fig. 367). In typical spinal nerves of higher vertebrates the dorsal root contains only the afferent fibers, whose cell bodies lie in the dorsal root ganglion.

In many segments of the trunk each spinal nerve is a discrete structure, inervating the axial muscles formed from the myotome pertaining to the segment and, as well, a corresponding strip of skin. However, in certain regions, notably opposite the paired limbs, there is an interweaving of branches of spinal nerves to form a pleasu (Fig. 360)—the brackial pleasus and himbosacral pleaus for front and hind legs, respectively. As a result we find that the muscles of any limb region may be supplied by fibers from several spinal nerves.

Constancy of Innervations, Nerre Grouth. Even in complicated limb pleatures we find that there is a high degree of constancy in the pattern of innervation of a given muscle in different animals, and there arose the doctrine that innervation is an absolutely constant feature—that a given muscle is always, over long evolutionary lines, innervated by the same nervous elements and by similar pathways. Actually, however, there are notable (although relatively rare) cases in which such a doctrine cannot be maintained. Any discussion of this problem leads to a consideration of nerve growth.

Of peripheral nerve fibers, the efferent elements grow outward toward the muscles which they innervate from cell bodies situated within the cord. Very likely in vertebrate ancestors the afferent cells were similarly contained in the cord. In most vertebrates, however, most such cell bodies are derived from the neural crest of the embryo (Fig. 64, p. 101); they migrate downward to form the spinal ganglia and send fibers both inward to the cord and outward to the periphery. In the head region part of the ganglia are derived from thickenings—placodes—in the ectoderm lateral to the forming neural tube and crest.

In what fashion do these peripheral fibers grow outward from cord, brain or ganglia to reach their end organs, sensory or motor? Some investigators have assumed that there is a sort of specific, mystic affinity between a special nerve fiber and a special organ to which it attaches, so that the nerve fiber "finds its mate."

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That there is some degree of specific association is certain since, for example, efferent axons do not attach to sensory structures nor afferent fibers to muscle cells. Experimental work, such as that on transplantation of salamander limb buds, shows that the presence of muscle materials does attract nerve fibers, but not necessarily those which would innervate them in a normal condition. It would seem that in great measure fibers tend to push out from the nerve ord along paths of least resistance in the microscopic structural pattern of surrounding materials. Since in successive generations the topography of a region will tend to be the same, given nerve fibers will tend to follow similar courses and thus bring about an essential constancy of innervation without the necessity of postulating precise specificity.

Nerre Components and Spinal Nerre Composition (Fig. 365.). Highly useful in the study of both peripheral and central nervous systems is the doctrine of nerve components. This points out that both afferent and efferent fiber types can be divided into somatic and risceral components. Somatic afferent fibers carry in sensations from the skin and muscles—the exterceptive and proprioceptive groups of the physiologists. Visceral afferents, on the other hand, bring impulses from the interceptive sensory structures of the gut and other internal structures. On the motor side, somatic efferents run to striated muscles of the somatic group in the "outer tube." of the body and limbs, sieceral efferents supply the visceral musculature of the gut region and smooth muscles and glands in various positions. There are thus four components in any normal spinal nerve, typically the two sensory components traversing the dorsal root, the two "motor" clements in the ventral root, all four unite in the base of the nerve trunk (Fig. 365, A).

It is of interest, however, that as we descend the vertebrate scale we find, increasingly, a departure from this two-and-two system. There is a tendency, representing (it would seem) a primitive condition, for visceral motor fibers to emerge via the dorsal root, thus giving a three-to-one situation (Fig. 365, B, C). Even in mammals there is evidence that some visceral motor fibers utilize the dorsal rather than the ventral root for emergence, and in amphibians and jawed fishes visceral motor fibers appear to be common in the dorsal root. Correlated with this, it would seem, are contrasts in spinal nerve structure. In most vertebrate groups dorsal and ventral roots are completely united distally and emerge at the same level of the cord. But in lower fishes the roots tend to alternate in position; in sharks and hagfishes the two roots are incompletely united; and in lampreys, finally, dorsal and ventral roots do not connect at all and are quite separate nerves (Fig. 368). This is probably the primitive condition and is a logical arrangement. The ventral roots here carry mainly or exclusively somatic motor fibers and lie opposite the muscle segments which they supply; the dorsal roots carry all sensory fibers and most or all visceral motor elements and (reasonably) make their way outward between muscle segments. Although this condition is, we have noted, much modified in most vertebrates by union of dorsal and ventral elements and transfer of the visceral component to the ventral root, we find today retention of this primitive system of dorsal and ventral nerves in the arrangement of certain of the cranial nerves.

#### VISCERAL NERVOUS SYSTEM

In the remote ancestors of the vertebrates the nervous system presumably consisted of two more or less discrete portions: one, a lowly organized set of superficial structures which responded to external stimuli; the other, a network of cells and fibers around the gut and other internal organs which enabled them to adjust directly to internal conditions. In vertebrates the more superficial portion of the nervous system has become highly organized and dominant. The old gut system persists, and there is evidence that to some degree the gut may still make local responses to internal stimuli. But with the rise of the external central nervous system of cord and brain, these structures have tended, so to speak, to conquer the nerve system of the viscera and in great measure to do away with its independence. In higher vertebrates, particularly, effective connections have been established and much visceral activity is mediated by cord and hypothalamic centers in the brain. But, as we are well aware from personal experience, visceral sensations and motor responses to them are not generally associated with the higher centers of the brain; we "know" little of what our viscera feel and have little conscious control over them.

The efferent pathways of the visceral system call for little remark. Fibers from gut sensory endings ascend to spinal cord and brain through special visceral nerve trunks discussed below or through the vagus nerve of the cranial system, which extends much the length of the gut.

The Autonomic System (Figs. 371, 373). Certain special efferent visceral pathways from the brain to the striated muscles of the branchial arch system will be discussed later. More complicated in structure are the efferent fibers which innervate the smooth muscles and glands of the body. These fibers constitute the autonomic system, in reference to the generally self-governing nature of their reflexes. A classification is as follows:

$$\label{eq:Visceral nervous system} \begin{cases} \text{Afficent} \\ \\ \text{Efferent} = \text{Autonomic} \end{cases} \begin{cases} \text{Sympathetic} \\ \\ \text{Parasympatheti} \end{cases}$$

The course and nature of the efferent pathways from the cord to the end organ differ notably from that described earlier for somatic motor fibers. The visceral impulse utilizes two neurons in succession. The first, the preganglionic neuron is comparable to a somatic element, its cell body lies in the cord; its axon is well myelinated. In a typical body segment this axon, after leaving the cord and entering the nerve trunk, leaves it shortly to descend ventrally in a risceral armus for communicating ramus) (Figs. 365, 369). It extends, however, only part way to the effector organ, muscular or glandular, for at some point along its course it enters a ganglion of the autonomic system. Here the impulse is relayed to a second, postganglionic neuron, whose axon (usually with little myelin in its sheath) completes the passage to the end organ. These postganglionic neurons are derived from the embryonic neural crest, descending along the developing nerves.

In higher vertebrates a combination of anatomic and physiologic investigations indicates that the autonomic system can be sorted out into two subdivisions, termed (1) sympathetic (in a narrow sense) or thoracolumbur system and (2) the parasympathetic or craniosacral system (Figs. 370, 371). All important organs

<sup>\*</sup> There is wide variation in the use of the terms concerned. The term sympathetic has been defined by various authors (e) narrowly, as here; (b) as equivalent to autonomic; (c) as equivalent to the entire visceral ("vegetative") system, both afferent and efferent. As still another confusing variant in terminology. "autonomic" is sometimes used for the entire visceral system, afferent as well as effects.



Fig. 367. Diagrams to show the distribution of nerve componens in doesal and ventral spinal roots, Smote sensory, steed as the sensor of the contraction of the contr

receive a double innervation from both systems. The two differ both functionally and topographically (although the functional differences are not absolutely clearcut). Stimulation of true sympathetic nerves tends to increase the activity of an animal, speed up circulation and slow down digestive processes, and, in general, make it fit for fight or frolic. The action of the parasympathetic, on the other hand, tends to slow down activity and promote digestion and a "vegetative" phase of existence. The postganglionic neurons of both systems stimulate their muscular or other end organs by giving off neurohumors from the fiber tips. In the sympathetics the materials produced are noradrenalin and adrenalin, hormones also produced (as noted in Chapter 17) by the adrenal gland; in the case of the parasympathetics it is the chemical known as acetylcholine. Still further points of contrast are anatomic. In a mammal the sympathetic outflow is from the thoracic and lumbar regions of the cord; parasympathetic fibers are associated with cranial nerves-notably the vagus -plus a second outflow in the sacral region. Another anatomic difference lies in the fact that in the sympathetics the relay to the second neuron takes place in ganglia close to the backbone or, at the farthest, in the dorsal mesentery not far below it. whereas in the parasympathetic system the first neuron runs all the way from brain or cord to a ganglion in, or close to, the organ concerned.

Most of the development of the complex autonomic system seen in mammals appears to have taken place gradually in the upward course of vertebrate evolution. In teleosts and all tetrapods the visceral rami of the trunk nerves enter the ganglia

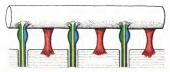


Fig. 368. Diagram of the spinal cord and nerves of the left side of a lamprey seen in dorsal view (anterior end to the left), to show the alternating arrangement of separate dorsal and ventral spinal nerves, related to intermyotomic spaces and myotomes. Nerve components colored as in Fig. 367.

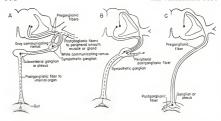


Fig. 369. Diagrammatic cross sections to show the path of autonomic filters. A. Sympathetic (thorsculmard) distribution in a nammal, with autonomic gaugiti nob in a lateral which in a dair an subswerberla position. Preganglionic filters may be relayed in other position and run crither to superficial structures with the major enercy transks or to the viscent, in both cases with a long postgraphonic neuron. B. Sympathetic distribution as found in many lower vertebrates; there is little development of a sympathetic chain, and no distinction of gaugiti into two groups; there to perspict and structures course independently or with distributions as found in many lower vertebrates; there is lattle development of a sympathetic them, and no distinction of gaugiti into two groups; there to perspict only structures cover independently or with the properties of the structure of the superficient of the superficient structures of

of the sympathetic chain which runs along either side of the backbone and gives off secondary neurons to peripheral areas, notably blood vessels; no such structures exist in lower fishes. In lower vertebrates, such as sharks (Fig. 373), there is no regional sorting-out of sympathetic and parasympathetic types and relatively little of the system of double innervation.

## CRANIAL NERVES

In the head region there is present a special series of varied nerves which are, particularly at first sight, difficult to compare with those of the body (Fig. 372). They were first studied in man and given names and numbers based on their mammalian functions and positions. Although, as we shall see, the human arrangement does not hold throughout, we shall introduce the study of cranial nerves by listing them.\*

- Olfactory: sensory, from the olfactory epithelium.
- II. Optic: sensory, from the eye.
- III. Oculomotor: innervates four of the six eye muscles.
- IV. Trochlear: to the superior oblique muscle of the eye (sometimes termed the trochlear muscle).
  - V. Trigeminal: a large nerve with three main branches, mainly bringing in somatic sensations from the head, with motor fibers to the jaw muscles.

<sup>\*</sup> The initial letters of the names of the cranial nerves are the initial letters of the words of the following choice bit of poetry: "On old Olympus' towering top a Finn and German viewed a hop."

VI. Abducens: to the posterior rectus muscle (which abducts the eye).

VII. Facial: partly sensory, but mainly important in mammals as supplying the muscles of the face.

VIII. Acoustic: sensory, from the internal ear.

IX. Glossopharyngeal: a small nerve, mainly sensory, and innervating (as the name implies) much of the tongue and pharynx.

X. Vagus: a large nerve, both sensory and motor, which (as the name suggests) does not restrict itself to the head region but runs backward to innervate much of the viscera—heart, stomach, and so forth.

X1. Accessory: a motor nerve accessory to the vagus.

XII. Hypoglossal: a motor nerve to the tongue muscles.

One can brutally memorize such a list of cranial nerves and their functions, but no one interested in the nervous system can stop at this point. We have here a series of nerves which are amazing in variety and seemingly haphazard in distribution, and one cannot but attempt to "make sense" out of them. Is there any logic in their distribution? Can they be grouped in any sort of natural eategories?

A clue to classification lies in a consideration of nerve components (cf. Table 3). We have noted that in the postcranial region, nerve components of four types are present. These are represented in the cranial region as well, but in addition, nerves to nose, eve and ear form a special somatic sensory group, and on the visceral side there are special types among both sensory and motor components. Taste fibers are considered as a special risceral sensory component, and the nerve supply to the striated visceral muscles of the jaws and gill region is quite unlike the autonomic system, forming a special risceral motor category. We thus have seven

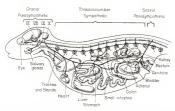


Fig. 370. Diagrammatic representation of the autonomic system of a mamual, Only a fraction of the true number of trush segments is represented. A symaphetic chain is developed, allowing exchange of there between segments. Symaphetic gauglia are represented by circles; short nerves projecting from them represent gary armi rejoining the main segmental never trush call maning to peripheral structures. There is here a regional sorting out of autonomic nerves into parasympathetic elements associated with crunial and surfal curves, and symaphetic nerves arising from trush segments. The two systems nearly one of the complex of the comp

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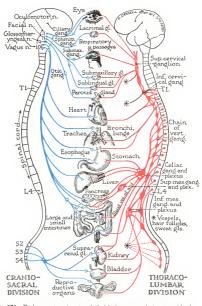
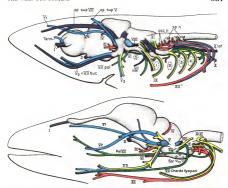


Fig. 371. The human autonomic system. At the left, the parasympathetic system; right, the sympathetic system. (From Millard, King and Showers, Human Anatomy and Physiology.)



types of components, as listed in the table. We can group cranial nerves into three types which (as indicated by the double rutings) show essentially clear-cut distinctions as to the components present. These three are (a) special sensory nerves of somatic type—1, II, VIII, and lateral line nerves; (b) dorsal root or branchial nerves, containing sensory components and special visceral motor components associated with the branchial region; and (c) ventral root nerves containing almost exclusively somatic motor fibers. The first category is peculiar to the cranial region; the other two are comparable to the dorsal and ventral roots of spinal nerves of lower vertebrates, and especially comparable to the separate dorsal and ventral nerves seen in lampreys and present in Amphioxus as well.

Special Sensory Nerves. In all vertebrates the three main sense organs

—nose, eye and ear—are innervated by special nerves; in primitive aquatic vertebrates we find also special nerve trunks for the lateral line organs.

Olfactory (I). As mentioned previously (p. 344), the olfactory is not a typ-

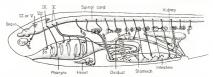


Fig. 473. Diagrammatic representation of the autonomic system of a shark. As in Figure 370, only a fraction of the true number of trank segments is represented, and "samples" only of types of innervation of abdominal viscers and blood vessels are given. Trank sympathetic ganglia are developed—indicated by white circles—and are usually associated with rend hodies (stippled). There is no development of a sympathetic chain, no development of garsy arms to peripheral structures, and no regional sorting out of sympaflectic and parasympathetic systems (cf. Fig. 370). Preganglionic autonomic nerves in full line, postganglionic nerves or fibers in broken line, (After L. X voun, modified.)

ical nerve, for its fibers come from the sensory cells of the nose and run inward to the brain, rather than outward. In mammals (in contrast to many lower vertebrates) the olfactory is not a formed nerve but a number of discrete fiber bundles passing back through the cribriform plate. In animals with a well-formed vomeromasal organ (p. 346) a discrete branch develops for its innervation.

Optic (II). This was described previously (p. 354). As in the case of the olfactory, this is not a typical nerve, for its fibers run inward from the ganglion cells of the retina; further, we have seen, it is not properly a true nerve but a specialized brain tract.

Acoustic (VIII). A more normal nerve, supplying the internal ear, its fibers arise from true ganglion cells, although these may be in part situated well peripherally, close to the sensory structures.

Lateral Line Nerres (cf. Fig. 347, p. 357). We have noted that the lateral line organs are intimately related to the auditory sense, and hence it is reasonable to find that the nerves to these structures are closely associated with the acoustic nerve. In fishes there are two major lateral line nerves, arising from the medulla anterior and posterior to the acoustic. The anterior nerve supplies much of the lateral line organs of the head; the posterior supplies the neuromasts of the occipital region and trunk. The anterior element accompanies the facial nerve, and most or all of the posterior nerve emerges with the vagus; the two are sometimes reckoned as part of the nerves which they accompany, but the association is merely one of "convenience," and the lateral line nerves are basically independent structures.

Branchial Nerves. We have noted that dorsal and ventral nerve roots were primitively distinct nerves and that the dorsal nerves carried not only all sensory components but the visceral motor elements as well. If Table 3 is inspected, it will be seen that a large series of cranial nerves appears to belong to this dorsal category—they lack somatic motor elements, contain sensory fibers and for the most part include a visceral motor component as well. This series includes the terminal nerve, profundus nerve, trigenimus proper, facial, glossopharyngeal and vagus (Fig. 374). The dorsal root series of cranial nerves, however, differs in one major respect from trunk dorsal roots, for they supply the region of the gill slist and

are primitively arranged, as branchial nerves, in a segmental pattern corresponding to the distribution of the gills. The glossopharyngeal nerve of fishes (Fig. 375) is a "model" member of this series. It is primarily associated with the first typical gill slit, and its main trunk descends posterior to this opening as a post-time motic ramss. In addition there are a small pretrematic rams, a pharyngeal mass reaching the roof of the pharynx, and a dorsal ramsa (which may be absent) to the skin. The gill slits back of the first generally have, in fishes, quite comparable nerves, but they all connect with the brain via a single large compound nerve, the vagus. More anteriorly in ancestral vertebrates there were probably three "normal" gill slits with typical branchial nerves comparable to the glossopharyngeal, but in all living forms the peculiar modifications of the jaw region have brought about marked specializations of the nerves in this region.

Terminal Nerve. In members of every vertebrate class except cyclostomes and birds there is found a tiny nerve which runs from brain to nasal cavity but is not olfactory, although apparently sensory in nature. Possibly it is a remnant of a most anterior member of this series which primitively innervated the mouth

region.

Profundus Nerre (V<sub>3</sub>). The ophthalmicus profundus nerve is a stout trank which receives somatic sensations from the "snout" region. In manunals it is intimately associated with the trigeminus and counted as the first of its three tranks, but in lower vertebrates it is often quite independent. It appears to have been in the ancient ostracoderms a typical "complete" branchial nerve, associated with a gill slit which was lost when the mouth opening expanded.

Trigeminal Nerve  $(V_{s}, V_{s})$ . The trigeminal nerve proper is believed to have been associated with a second gill slit, present in ostraodems, but, like the first, lost when the mouth expanded its gape in developing a jawed condition. In contrast to the profundus, however, it has remained haighly developed and innervates the jaw muscles as well as having a somatic sensory component. There are two principal branches, the maxillary and mandibular rami, somewhat comparable to pre- and post-trematic rami of more posteror gill nerves.

Facial Nerre (VII). This is the nerve proper to the spiracular gill slit, and in fishes it usually has a fairly normal branchial nerve construction. We have noted earlier that in mammals the muscles proper to this arch have spread over head and face as the muscles of expression; the facial nerve owes its name to their innervation.

Glossopharyngeal Nerve (IX). As noted, this small nerve is associated in fishes with the first gill slit; it is persistently small and unimportant in tetrapods.

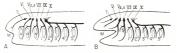


Fig. 3.74. Diagrams showing the distribution of branchial (dorsal root) cranial nerves. A, Hypothetic pramitive condition, with typical nerves to each of two anterior gill slits lost in jawed vertebrates, and a terminal nerve to anterior end of brade B. Condition in jaw-bearing fashes. M, Mouth; O, O', anterior gill slits lost in gnathostomes; S, spiracular slit; T, terminal nerve; 1 to 5, typical gill slits of gnathostomes.

Nerve Types	Special Sensory	Branchial (Dorsal)					Ventral
Components	Special Somatic Sensory	General Somatic Sensory	General Visceral Sensory	Special Visceral Sensory	Special Visceral Motor	Visceral Motor (Autonomic)	Somatic Motor
O. Terminalis	4 3	Х		-	_		
I. Olfactory	х			1			
II. Optic	X						
III. Oculomotor	3		-	15		(X)	х
IV. Trochlear	1			- 1			X
V <sub>1</sub> . Profundus		х				(X)	
V <sub>2</sub> , <sub>3</sub> . Trigeminal proper	3	х		K	х		-
VI. Abducens				1			х
VII. Facial	L	(X)	Х	X	х	x	(
VIII. Acoustic	A			1			
IX. Glossopharyngeal	L	(X)	х	X	x	x	
X and XI. Vagus (and accessory)	L	x	х	x	x	x	
XII. Hypoglossal	Jean		:	-			х

Proprioceptive filters (muscle sense) are not included. L. Lateralis sensory components of lower vertebrates (in X, the vagus, alone in amphibians); A, acoustic component of lateralis-acoustic system. Components in parentheses: variable or negligible. The three areas between vertical double-ruled lines indicate the components proper to each of the three nerve types. Except for the usual presence of autonomic fibers accompanying the occlusionest nerve, the distinctions are clear-out.

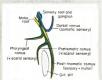
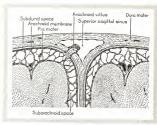


Fig. 375. Diagram showing the composition of a typical branchial nerve, such as the fish glossopharyageal. The three nerve components colored as in Figs. 367 and 372.

Fig. 37-6. Transverse section of a portion of the brain of a manual to she the meniages. The section is taken through the meniages. The section is taken through the partition (talls cerebri) between the two cerebral hemispheres. The superior signification of the section of the tall the section of the offers a minor means for transition of material section of the section of the section of the offers a minor means for transition of the section of



Vagus Nerve (X, XI). This is the largest and most versatile of the cranial nerves; the separately named accessory nerve of mammals is essentially a postetior motor root of the vagus. There is usually a small skin sensory branch, but the vagus is essentially a visceral nerve. In fishes the vagus supplies all the gill arches behind that of the first typical gill; in addition a powerful visceral ramus extends backward along the gut as a major element of the autonomic system.

Somatic Motor Nerves. The nerves in this category—III, IV, VI and XII of the human series—are highly comparable in most regards to primitive ventral roots of spinal nerves. They are almost entirely composed of somatic motor fibers and innervate striated muscles derived from somites. There have been attempts to align these nerves with members of the branchial series as ventral and dorsal nerves of a single segmental series. But these attempts are, I believe, pointless; for the segmentation to which the somatic nerves are related is that of the body somites, whereas the segmentation to which the branchial nerves correspond is that of gill slits. There is no evidence that somite and gill slit series have any necessary relationship to one another.

Eye Muscle Nerves (Oculomotor, Trochlear, Abducens) (III, IV, VI). These small nerves innervate the eye muscles derived from the three head somites (cf.

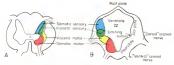


Fig. 377. Diagrams showing the distribution of sensory and motor columns, Somatic enterpressory association column, blue viscoral suscers, general viscoral mater column, alphae, somatic motor, ord. At Buspinal cord of the adult of certain lower vertebrates. H. The embranic modalit oblongate, the embryonic england ord shows a similar arrangement of the columns. The plate of tissue bying below the limiting splans is termed the foor plate from this, motor centers arise. The sensory region above is the "wing" or alar plate. (Partly after Herrick)

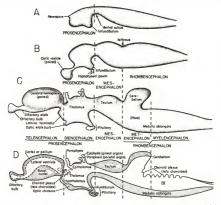


Fig. 378. Diagrams to show the development of the principal brain divisions and structures. A. Only prosencephalon (primitive forebrain) distinct from remainder of neural tube. B. Three main divisions established. C. More mature stage in lateral view. D. The same in median section. (Partly differ Bistehlis)

p. 208). The little trochlear is unusual in that it curves upward within the substance of the brain stem and emerges dorsally to supply the muscle of the opposite side of the head.

Hypogloszal (XII). In fishes (particularly among sharks) the posterior end of the skull—and hence of the caraial nerve series—it not a fixed point, for the occiput is formed by a variable number of vertebrae. There is, hence, a variable number of occipital regress, which are essentially anterior members of the trunk series but tend to lose their dorsal roots, and mainly supply muscles formed from the somities of the occipital region. In amniotes the condition is stabilized; back of the vague, (and accessory) there is a final caraial nerve, the hypoglossal, usually formed by three ventral roots which presumably represent three body segments fused into the occipital region. There is no hypoglossal nerve in modern amphibians, but fossil evidence shows it to have been present in early amphibians as a direct inheritance from the occipital revies of the shs. (In this regard, as in many others, modern amphibians are degenerate rather than primitive.) We have noted that the myotomes of the general occipital region migrate in the embryo backward and downward around the gill region to form the hypobranchial musculature of feterpook (Fig. 179, p. 204).

Trunks of occipital nerves in fishes follow the muscles in this movement, and in amniotes the hypoglossal nerve follows a similar path, back, down and then forward around the pharvageal region to innervate the tongue musculature.

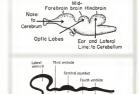
#### CENTRAL NERVOUS SYSTEM-ACCESSORY ELEMENTS

Ordinary connective tissue is not present in the central nervous system, but as differentiation of the neural tube occurs in the embryo, a part of the cells present become specialized for supporting rather than nervous functions. A fraction of them remain around the borders of the cavities of the brain and cord and retain an epithelial formation, but most are small star-shaped cells termed neuroglia scattered among the neurons.

Brain and cord are not merely protected by the braincase and the neural arches of the vertebrae, but are further enabetabled in one or more wrappings, the meninges (Fig. 376). In most fishes there is but a single meninx of complex structure, but in all tetrapods at least two are present. The outer, the dura mater, is a stout sheath, mainly of connective tissue origin; it is connected by slender filaments with a softer inner membrane, derived from the neural crest, which is applied to brain or cord. In mammals this inner membrane is divided into two delicate structures, an outer arachnoid and an inner pia mater, the two separated by a fluid-filled subarachnoid space crossed by a colweb of delicate tissue threads.

The tube present in the neural canal of the embryo persists in the adult as the ventricles of the baria and central canal of the spinal cord. These cavities (and the subarachnoid space in the meninges) are filled by a clear liquid, the cerebrospinal fluid, similar in composition to the interstitial fluid or the perilymplatic liquid of the car. Materials may reach it from the blood through the medium of special vascular structures, notably the choroid plexuses of the brain (p. 398).

Fig. 379. Diagram to show the relation in lower vertebrates of the three major sense organs to the three dorsal areas of gray matter in the three major subdivisions of the brain. (In mammals the midbrain tectum is reduced and optic sensations are relayed to the cerebrum instead.)



Midbrain Hindbrain

Fig. 380. Diagram showing position of brain ventricles. (From Gardner.)

388 THE VERTEBRATE BODY

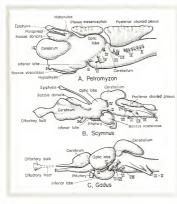


Fig. 381. Lateral views of brain of A, a lamprey; B, a shark; C, a codfish. In the lamprey an exceptional condition is the development of a vascular choroid area, the plexus mesencephali, on the roof of the midbrain. (After Büstehli, Allborn)

#### SPINAL CORD

The spinal cord (Figs. 364, 365, pp. 372, 373, 377), which runs the length of the body, is a little-modified adult representative of the nerve tube formed in the early embryo. A small liquid-filled central canal persists, Suboval or circular in lower vertebrates, the cord tends to expand in bilateral fashion in higher forms. Two layers can be readily distinguished, a central area of gray mater, mainly composed of cell bodies, and a peripheral white matter, formed of countless myelinated fibers coursing up and down the cord. The gray substance was, it seems, primitively arranged in a fairly even fashion about the central cavity, but in most vertebrates it has a symmetric arrangement which in section has an H-shape or that of a butterfly's wings. There thus appear to be a pair of "horm" on either side; actually, of course, each "horn" is merely a section of a longitudinal structure, and we should speak rather of a dorsal column and a ventral column.

The ventral column is the seat of the cell bodies of efferent neurons of the spinal nerves. Their numbers will vary, of course, in any given part of the column with the volume of musculature at that level, and in land vertebrates this column is much expanded in the regions supplying the limbs. The visceral efferent neurons are situated above and lateral to those of the somatic type and sometimes are distinguished as a lateral column.

The dorsal column is associated with the dorsal, sensory nerve roots and is

the seat of the cell bodies of association neurons through which impulses brought in from sense organs may be relayed and distributed. The arrangement of various clusters of association neurons is complex and variable, but in some cases (particularly in certain embryos) we can distinguish a larger series associated with somatic sensory reception, situated dorsally and medially, and a smaller visceral sensory group placed more ventrally and laterally. There thus appear to be in the gray matter four areas on either side related to the four major nerve components, being in sequence from dorsal to ventral! somatic sensory, visceral sensory, visceral motor, and somatic motor. It is of interest that the same arrangement is found in the gray matter of the brainstem (Fig. 377).

The white matter is composed of ascending and descending fibers of sensory nerve cells, of similar fibers which take origin from the association cells, of fibers which carry sensory stimuli forward to the brain, and of fibers returning from brain centers to act on motor neurons. The last two categories are especially abundant in higher vertebrate groups, in which the trunk is more completely under the influence of the brain than it is in lower forms. Topographically the "horns" divide the white matter into dorsal, lateral and ventral funiculi; more important are restricted areas within the funiculi occupied by specific fiber tracts with a given type of function and connections; but these vary too much from group to group to be described here in detail.

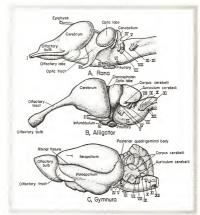
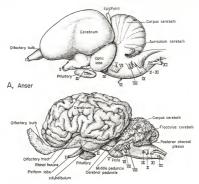


Fig. 382. Lateral views of brain of A, a frog: B, an alligator; C, an insectioner representing a primitive mammalian type. (In normal head posture the front end of the alligator brain is tilted upward. (After Bütschli, Clark, Crosby, Gaupp, Wettstein.)



### B. Equus

Fig. 383. Lateral views of brain of A, a goose; B, a horse. (The goose brain, like that of the alligator, is filted upward anteriorly in life.) (After Bütschli, Kuenzi, Sisson.)

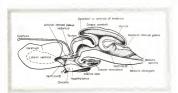


Fig. 384. Right half of the brain of a shark (Scyllium) in median aspect. Unshaded areas are those sectioned. (After Haller, Bruckhardt.)

#### THE BRAIN

In all vertebrates, as well as in the more highly organized invertebrates, we find a concentration of nervous tissue at the anterior end of the body in the form of a brain. Such a concentration is to be expected, for in an active bilaterally symmetric animal it is this region which first makes contact with environmental situations to which response must be made, and in which, hence, sense organs and associated nervous structures are most advantageously situated.

Brain Architecture. Primitively, we may believe, the brain was merely

a modestly developed anterior region of the neural tube where, in addition to local reflexes, special sensory stimuli were assembled and "referred for action" to the semiautonomous body region via the spinal cord. Within the vertebrates, however, there has occurred a strong trend for the concentration in the brain of command over body functions, with the development of a series of complex centers. We have noted, in discussing the elementary composition of the nervous system, the way in which the intercalation of an association neuron into the simple reflex arc greatly broadens the field of possible responses to a sensory stimulus and, conversely, greatly increases the variety of stimuli which may excite a specific motor response. The brain pattern is essentially an elaboration of this principle-the interposition of further series of neurons between primary areas of sensory reception and final motor paths. These intermediate neuron groups are clustered in functional centers. In such centers afferent impulses may be correlated and integrated for appropriate responses or motor mechanisms coordinated; on still higher levels there may develop association centers of whose activity memory, learning and consciousness may be the products.

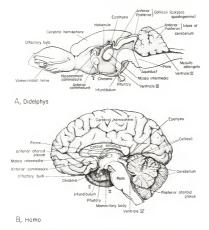


Fig. 365. Right half of the brain, in median aspect, of A, an opossum; B, man. Unshaded areas are those sectioned. The internally hulging side walls of the diencephalon may meet and fuse in the midline, forming a "massa intermedia," which, however, has no functional importance. (A after Loo.)

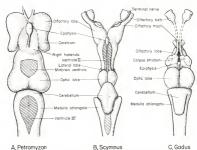


Fig. 386. Dorsal views of the brain of A, a lamprey; B, a shark; C, a teleost (codfish). Hatched areas are those in which a choroid plexus has been removed, exposing the underlying ventricle. (After Butschli. Ahlborn.)

In the present very elementary account our attention will be mainly centered on external features and gross structures of the sort seen in Figures 381–389. But while such superficial aspects of brain anatomy are significant, an adequate understanding of the working of the brain can no more be gained from them than a knowledge of a telephone system can be had from an acquaintance with the external appearance and room plan of the telephone sexchange building. What is important in a telephone system is the wring arrangements and switchboards; in a brain it is the centers in which various types of activities occur and the tracts of fibers connecting these centers.

It may well be that the brain "wiring" was primitively much like that of the spinal cord-a general crisscross of fibers interconnecting all areas. To some degree there does persist in the brain a certain amount of seemingly random distribution of fibers, and there is further a persistence of a primitive condition in the reticular system, a band of interlacing cells and fibers carrying motor impulses along the motor columns of the brain stem (seen diagrammatically in Figures 399-401). In general, however, there is a strong tendency for the clustering together of nerve cells in centers and the assembling of fibers with like connections into definite bundles. Although certain special centers have special names, most are termed ganglia or nuclei (making an unfortunate duplicate biologic use of the latter word). Fiber bundles connecting nuclei with one another or with the cord are in general termed tracts; the fibers of a tract are, of course, axons of neurons whose cell bodies lie in the nucleus of origin. The brain is constructed on an essentially bilaterally symmetric pattern; in consequence, cross-connections of fiber bundles, termed commissures, must be present between the two sides in order that the animal may not, literally, have a dual personality.

THE NERVOUS SYSTEM 393

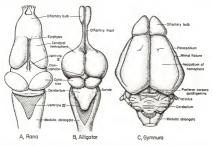


Fig. 387. Dorsal views of the brain of A, a frog: B, an alligator; C, a tree shrew. Hatched areas are those in which a choroid plexus has been removed, exposing the underlying ventricle. (After Gaupp, Crosby, Wettstem, Clark.)

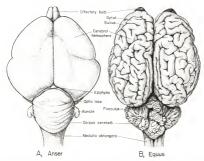


Fig. 388. Dorsal views of the brain of A, a goose; B, a horse. (After Bütschli, Kuenzi, Sisson.)

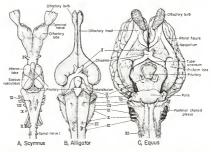


Fig. 389. Ventral views of the brain of A. a shark; B. an alligator; C. a horse. (After Butschli, Wettstein, Sisson.)

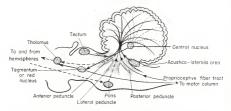


Fig. 390. Diagram to show the main connections of the cerebellum. The connections with the cerebral cortex, peculiar to mammals, are shown in broken line.

Brain Development (Fig. 378). The general topography of the brain and its parts is best understood through a consideration of its development. The brain develops rapidly in the embryo—much more rapidly than almost any other organ—and there is early established a generalized structural pattern upon which the numerous variations seen in the adult brains of different groups are superposed. In early stages the future brain is merely an expanded area of the neural tube. Presently its anterior end tends to fold downward, producing a cephalic flexure, and a bit later there is a constriction more posteriorly at a point known

as the sistmus. There is thus established a division into three major brain regions termed, in front-to-back order, the prosen-ephalon, mesencephalon and homben-cephalon—in plain English, forebrain, midbrain and hindbrain. Although various specialized outgrowths are later added, the original "hublar" portions of these three brain "segments" are still recognizable in the adult, where they are collectively known as the brain stem, here are persistently located centers for many simple but basically important neural functions. The lengthwise division of the brain stem into three portions is correlated with the fact that in most vertebrates each of the three is associated with one of the three major sense organs: nose, eye and ear and lateral line (Fig. 379). In each region there develops from the stem a dorsal outgrowth of layered "gray matter" which is primitively associated with one of these sensory structures. These are, in anteroposterior order: the cerebal hemispheres of the prosencephalon, primarily associated with smell; the midbrain roof—tectum—associated with vision; and the cerebellum, a hindbrain outgrowth a sociated with the ear and lateral line.

By the time the three primary subdivisions are established special structures have begun to make their appearance in the forebrain. The optic vesicles, discussed in the last chapter, push our from its floor. More posteriorly, there is a down-growing median projection, the infundibulum; concomitantly, a pocket of epithelium, the hypophysed pouch (Rathke's pouch), grows upward from the roof

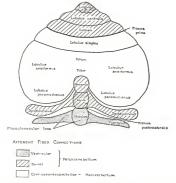
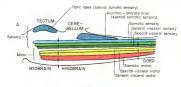


Fig. 391. Dagram of a surface view of a mammalian cerebellum (showing details not discussed in the twst). The stopped and hatched portions, associated with equilibrium (vestibular) and with muscle sensations (spinal), are the phylogenetically oldest parts of the cerebellum; the white area is a mammalian addition associated with the cortex of the cerebral hemispheres. (From Fulton, after Larsell.)



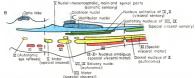


Fig. 392. Diagrams of midbrain and hindbrain regions in lateral view to show the arrangement of sensory and motor nuclei. Somatic sensory, red; special somatic sensory, stippled; visceral sensory, green; special visceral sensory, hatched; visceral motor, yellow; special visceral motor, stippled; somatic motor, red. A. Hypothetic primitive stage, in which brain stem centers were continuous with one another and with the columns of the cord. Even at such a stage, however, it would be assumed that special somatic centers would have developed for eye and ear. The brain region includes a special visceral motor column for the branchial muscles. B, Comparable diagram of the mammalian situation. The somatic sensory column is still essentially continuous (almost entirely associated with nerve V), but the other columns are broken into discrete nuclei. The visceral sensory column includes both a general visceral nucleus (mainly for afferent fibers from the viscera via the vagus) and a special nucleus for the important sense of taste. Of efferent visceral nuclei, there are small anterior ones for autonomic eve reflexes and the salivary glands, and a large nucleus for parasympathetic fibers to the viscera via the vagus-There are important branchial motor nuclei for V, VI, and IX, X (ambiguus). The somatic motor col-

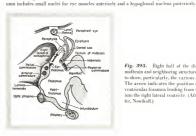


Fig. 393. Right half of the diencephalon, midbrain and neighboring structures of a lizard to show, particularly, the various outgrowths. The arrow indicates the position of the interventricular foramen leading from ventricle III into the right lateral ventricle. (After von Kupfer, Nowikoff.)

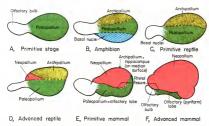
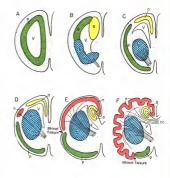


Fig. 394. Diagram to show progressive differentiation of the cerebral hemisphere (cf. Fig. 395), Lateral views of left hemisphere and olfactory ball. In I. the hemisphere is mercity an olfactory loke, R. Dorsal and ventral areas, archipallism (m. hippocampus) and basal nuclei (corpus striatma) are different tated. C. The basal nuclei have more for the inner part of the hemisphere. I. The neopallism appears as a small area (in many reptiles). E. The archipallism is forced to the median surface, but the neopallism areas tiell of modered dimensions, and the differency areas are still geometre below the rhand fissure (as in primital of modered dimensions, and the differency areas are in groundered below the rhand fissure (as in primital of median dimensions) and the differency areas are restricted to the ventral aspect, and the neopallisal areas are greatly enlarged (as in advanced manules). The versures either components of the hemispheres are distinguished for consecutions.

Fig. 395. Diagrammatic cross sections of left cerebral hemisphere to show stages in the evolution of the corpus striaturn and cerebral cortex. A, Primitive stage, essentially an olfactory lobe; gray matter internal and little differentiated. B. Stage seen in modern amphibians. Gray matter still deep to surface, but differentiated into paleopallium (= olfactory lobe), archipallium (= hippocampus), and basal nuclei (= corpus striatum), the last becoming an association center, with connections from and to the thalamus (indicated by lines representing cut fiber bundles). C. More progressive stage, in which basal nuclei have moved to interior, and pallial areas are moving toward surface. D, Advanced reptilian stage; beginnings of neopallium. E. Primitive mammalian stage; neopallium expanded, with strong connections with brain stem; archipallium rolled medially as hippocampus; paleopallial area still prominent. F. Progressive mammal: neopallium greatly expanded and convoluted; paleopallium confined to restricted ventral area as pyriform lobe. The corpus callosum developed as a great commissure connecting the two neopallial areas. a. Archipallium; b. basal nuclei; cc. corpus callosum; n, neopallium; p, paleopallium; V, ventricle. The different types of "gray matter" colored as in Fig. 39.1



of the mouth. In later stages modified infundibular tissues and those derived from the pouch come to form the pituitary gland or hypophysis. Dorsally there grows from the forebrain roof a series of median processes and a median "eye stalk" (sometimes two). Particularly striking and important is the development more anteriorly of paired dorsal forebrain outgrowths. These are hollow pockets of tissue which extend forward toward the nasal region; from them develop the cerbral hemispheres and, still farther anteriorly, the olfactory bulbs. These structures constitute the telencephalon, the anterior terminal segment of the brain; the unpaired part of the forebrain is the dincephalon.

Back of the forebrain region there are relatively few major modifications as development proceeds. The midbrain shows only a pair of dorsal swellings which form the tectum, prominent in lower vertebrates. In the hindbrain a dorsal outgrowth from the front part of the roof becomes the cerebellum. The brain stem here is little changed in the adult, where it is termed the medulta oblongata. In mammals, however, the part below the cerebellum is expanded into a structure termed the pons. Pons and overlying cerebellum are distinguished as the metacephalon from the most posterior part of the oblongata, the myelencephalon.

The principal brain structures of the adult may be tabulated according to the divisions established in the embryo:

Prosencephalon		Cerebral hemispheres, including olfactory lobes, basal nuclei (corpus striatum) and cerebral cortex (pallium); olfactory bulbs Epithalamus; thalamus; hypothalamus; and appendages
Mesencephalon		Tectum, including optic lobes (corpora quadrigemina in mammals); tegmentum; crura cerebri (cerebral peduncles) in mam- mals
Rhombencephalor	Myelencephalon	pons of mammais

Ventricles. The original cavity of the embryonic neural tube persists in the dult brain in the form of a series of liquid-filled cavities and passages (Figs. 380; 397, p. 402). A cavity, or lateral entricle, is present in each cerebral hemisphere; these communicate through small foramina with a median third venticle in the diencephalon. Within the midbrain there is in lower vertebrates a well-developed ventricle; but in amniotes this becomes a narrow channel, the cerebral aqueduct, leading back to a fourth ventricle areas of thin and highly folded vascular tissue, the choroid plexuses, through which exchange of materials takes place between the blood and cerebrospinal fluid.

Medulla Oblongata. Approach to the study of brain architecture is best mad most closely resemble the spinal cord. The brain stem is simplest in construction and most closely resemble the spinal cord. The brain stem is simpler than its specialized dorsal outgrowths, and in that part of it which lies in the hindbrain region, the medulla oblongata, we find a structure basically similar to the cord. THE NERVOUS SYSTEM 399

It is from the medulla (and the adjacent part of the midbrain) that there arise all the cranial nerves except the atypical ones from the nose and eye. The medulla itself is basically similar to a section of the spinal cord, except that the central canal is greatly enlarged to form the fourth ventricle and its roof is expanded to form the posterior choroid plexus. As a consequence the columns of gray matter are pushed apart to lie on either side of the ventricle. These columns (Figs. 377, A, p. 385; 390) are basically the four we have already seen present in the cord and arranged in the same order, with a horizontal sulcus separating the sensory columns above from the motor columns below. In the embryo the columns are simple in nature; in the adult, however, they tend (particularly in higher vertebrates) to break up into a series of nuclei of specialized nature, as indicated in Figure 392, B. These nuclei give us all the elements required for reflex circuits between sensory reception and the responding effector organs of the head and gill region. In addition, however, we find at the upper margin of the medulla a special area or set of nuclei which serve for primary reception of sensations from the ear and the primitively associated lateral line structures. In mammals, we have noted, there is a further specialization of the medulla in the development, anteriorly, of a swollen region, the pons, containing a great mass of neurons that, as noted later, relay impulses from hemispheres to cerebellum.

In lower vertebrates trunk and tail are to a considerable degree independent of the brain in their activities. In fishes and tailed amphibians, however, the medulla region contains the cell bodies of a pair of spectacular grant cells (cells of Mauthner) whose fibers extend the length of the cord and exercise control over the rhythmic movements of the trunk and tail, important in fish locomotion.

Cerebellum (Figs. 390, 391). Rising above the brain stem at the anterior end of the medulla is the cerebellum, a brain center, often of large size, which is of extreme importance in the coordination and regulation of motor activities and the maintenance of posture. It acts in a passive, essentially reflex fashion in equilibrium. Its function in regulating muscular activity may be compared to that of "staff work" in the movement of an army. To carry out the general orders of an army commander it is necessary that there be in hand information as to the position, current movements, condition, and equipment of the bodies of troops concerned. Similarly, a "directive" for muscular action coming from higher brain centers-say, for the movement of a limb-cannot be carried out efficiently unless there are available data as to the current position and movement of the limb, the state of relaxation or contraction of the muscles involved, and the general position of the body. Such data are assembled in the cerebellum and synthesized there, and resulting "orders" issued by efferent pathways render the movement effective. Although there are connections with various sensory centers, the data utilized by the cerebellum in primitive forms are derived mainly from two sources, the sensory structures in the body muscles and tendons, and the sensations arising in the equilibrium apparatus of the ear plus lateral line organs. We have noted that these last sensations have a primary reception center in the upper margin of the medulla; the cerebellum rises upward from this area and, indeed, appears to have originated historically from these acoustico-lateralis centers.

The cerebellum varies greatly in size and structure from group to group; its size is generally correlated with the locomotor agility of the animal. It is seen at the height of its development in birds and mammals, as shown in Figure 391. Its most ancient portions, phylogenetically, are the floculi, especially concerned with equilibrium and closely connected with the inner ear. In contrast to every

other area of the brain except the cerebral hemispheres and the midbrain roof, the cerebellum is a region in which there develops a cortex, a layered surface sheet of gray cellular material, complex in structure and often highly convoluted. The cerebellar cortex is connected with other brain areas by stout bundles of fibers which form its pedundes; these are shown in Figure 390. In mammals, but not in other classes, there are strong connections in both directions between the cerebellum and the cerebral hemispheres; the swollen pons is a relay point in the nath from bemispheres to cerebellum.

Midbrain and Diencephalon. In contrast with the posterior part of the brain stem, the mesencephalon and diencephalon show specialized features in vertebrates of all classes.

The midhrain side walls, termed the tegenentum, function mainly as the seat of centers and tracts carrying motor impulses down the brain stem from "higher" centers. The midhrain roof has had a checkered career. In all vertebrates except mannals the fibers of the optic nerve which enter the brain in the diencephalic region do not terminate there but run upward and backward to the midhrain roof, the tectum. This is an area of gray matter which in many vertebrates is highly developed. Primarily it is a visual center, but to it are attracted fiber paths from other sensory centers—from those of the ear and lateral line, from the somatic sensory areas and from the nose via the cerebral hemispheres. As a result, sensory stimuli from all somatic sources are here associated and synthesized and notor responses originated. The tectum thus appears to be in fishes and amphibians (where cerebral hemispheres are little developed) the true "heart" of the nervous system—the center which wields the greatest influence on body activity. In reptiles and birds the tectum is still an area of great importance but is rivalled, and in birds overshadowed, by developments within the hemispheres.

In mammals the tectum has undergone a startling reduction in importance; most of its functions have been transferred to the gray matter of the cerebral hemispheres, and most of the sensory stimuli which are integrated in the midbrain in lower vertebrates are in mammals projected, instead, to the cerebral cortex. Not even visual sensations are received here; the once important tectum is represented only by two pairs of small swellings, the corpora quadrigemina, which function only for eye reflexes and as a relay station for auditory stimuli on their way to the cerebral bemispheres.

The diencephalon, the region surrounding the third ventricle, has dorsal and ventral outgrowths of interest (Fig. 393). We have noted in the last chapter the frequent presence of median eye structures or their glandular representatives, such as the pineal organ. Here, too, are located the anterior choroid pleus and in some cases a thin-walled sac, the paraphysis, of unknown function. In the floor of the diencephalon is the optic chiasma, and in most fishes there is frequently a large vascular sac of uncertain function. Most important of diencephalic appendages is the pituitary gland or hypophysis cerebri, the major endocrine structure of the body, described in the next chapter.

The walls of the diencephalon are termed the thalamus, and this is in turn divided into the epithalamus, thalamus proper and hypothalamus. The epithalamus is of relatively little importance. The hypothalamus contains a number of nuclei which are the highest centers of the visceral nervous system. The range of their functions is incompletely known; it is, however, of interest that (for example) temperature regulation in birds and mammals and sleep in the latter class are controlled by the hypothalamus.

The thalamus proper is in lower vertebrates an area of modest importance but is in every case a relay area for impulses passing to and from the ecrebral hemispheres. The ventral part of the thalamus is a forward outpost of the motor columns of the brain stem and cord, and functions as a relay center for part, at least, of the motor impulses travelling downward from the hemispheres. The dorsal part of the thalamus is a sensory relay center for impulses travelling upward to the ecrebral hemispheres. In lower vertebrates, where the hemispheres are relatively undeveloped, this region is of no great importance. But in higher vertebrate groups where, as we shall see, the hemispheres come to be the dominant association centers, the functions of the dorsal halamus are pronounced. Skin stimuli and auditory stimuli are relayed upward through dorsal thalamic nuclei; and, still further, the optic nerve fibers, which in most vertebrates plunge through the diencephalon to the midbrain roof, in mammals are relayed here to the gray matter of the hemispheres.

Cerebral Hemispheres. The evolution of the cerebral hemispheres is the most spectacular story in comparative anatomy. These paired outgrowth of the forebrain hegan, it would seem, simply as loci of olfactory reception. Early in tetrapod history they became large and important centers of sensory correlation; by the time the mammalian stage is reached, the greatly expanded surfaces of the hemispheres have become the dominant association centers, seat of the highest mental faculties. The development of such centers in this area emphasizes the importance of the sense of smell in vertebrates, as we have seen, the acoustico-lateralis system and vision are senses upon which important correlation mechanisms were erected early in vertebrate history, but in the long run smell has proved dominant. Smell is of little account in higher primates, such as ourselves, but in most vertebrate groups it has been and is a major channel through which information about the outside world is received, and it is thus but natural that its brain centers should form a base for the erection of higher correlative and associative mechanisms.

The most anterior outposts of the brain are paired olfactory bulbs, in which fibers from the olfactory cells of the nose are received and relayed backward through an olfactory tract to the cerebral hemispheres. These structures are universally present but in fishes are usually relatively small and incompletely differentiated, and only the anterior parts of the hemispheres are paired. Primitively, as seen in cyclostomes, the hemispheres function merely in a fashion preserved in higher vertebrates only in that portion of the structures termed the olfactory lobes (Figs. 394, 4; 395, 4). In such areas olfactory sensations are relayed to the more posterior centers; few if any libers travel the reverse route from brain stem to hemispheres for correlation there.

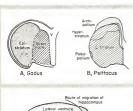
In a somewhat more advanced type of hemisphere such as that seen in amphibians (Figs. 394, B; 395, B) most of the tissues of the hemispheres can be divided into three areas, of interest because of their history in more progressive vertebrates. The gray matter of much of the hemispheres tends in these higher types to move outward from its primitive internal position to the surface and thus to become the cerebral cortex, or pallium ("cloak"). In amphibians the gray matter is still largely internal, but these terms may be used in the light of later history. A hand of tissue along the lateral wall of the hemisphere of a persistently simple offactory nature is the paleopallium, destined to form the offactory (pyrinorm) lobes of advanced types. Dorsally and medially is the archipollium, a some-

what more advanced correlation center destined to become the hippocampus in mammals and apparently related to "emotional" hehavior. Ventrally lies a large area of gray matter which persistently remains internal in the higher development of hemisphere structures; this forms the basal nuclei, the corpus striatum of mammals.

An aberrant type of forebrain seen in the teleosts may be parenthetically noted here (Fig. 396, 4). In these fishes there is none of the trend toward outward movement of the gray matter seen in higher tetrapods; on the contrary, the outer walls of the hemispheres are thin membranes and the cellular material is crowded into a mass bulging into the ventricles from below.

In reptiles (Figs. 394, C; 395, C) the hemispheres are advanced over those of amphibians both in size and complexity of structure. Some of the gray matter is trending toward a superficial position. The basal nuclei have moved inward to occupy a considerable area of the floor and are far from being purely olfactory in nature. Strong projection fiber bundles run upward to them from the thalamus and back from them to the brain stem; the basal nuclei are obvious correlation centers of importance. In birds (Fig. 396, B) this trend for development of the basal nuclei has progressed further. The bird hemispheres are large, but their development is due to enormous expansion of the basal nuclei, and the outer walls of the hemispheres are little development. It is obvious that the basal nuclei form a dominant association center in which, one may believe, are concentrated the mechanisms which evoke the complex "instinctive" action patterns seen in birds.

In mammals cerebral evolution has taken quite another course from that



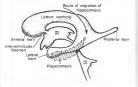


Fig. 396. Abbernat types of forchrains. See tion of left hemispheres of A, a teleoci (codish): B, a hird (parcot). In teleoats the root of the vontricles is only a membrane: the gray matter has been pashed downward and inward to join the bash andack (or striatum) as an epistratum. In high the cortex is little developed but there is a landagous to the teleoats) a great development of the hasal mackic (or corpus striatum); a dorsal (antagous to the teleoats) a great development energion terment the hyperstriatum is believed to be a correlation center of high order, r, Ventricle. Best annecia battle.

Fig. 397. The brain ventricles of an advanced mammalian type (Henon) in lateral view from the left. The ventricles are represented as solid objects, the brain tissue being removed. With expansion of the cerebral hemisphere, the lateral ventricle has expanded backward to a posterior horm in the occipital lobe, and downward and forward laterally to a lateral horn in the temporal lobe. With this hack ward and downward and the state of the state o

THE NERVOUS SYSTEM 403

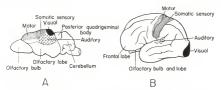


Fig. 398. Lateral view of A, the brain of a shrew; B, the cerebrum of man; to show cortical areas.

found in birds (Figs. 394, D-F; 395, D-F). The basal nuclei are moderately well developed in the interior of the hemisphere as the corpus striatum. The old fashioned olfactory cortex area, the paleopallium, persists as the relatively small pyriform lobes; the archipallium persists likewise as the hippocampus, a small area tucked away on the medial aspect of the hemisphere. In mammals emphasis is placed on a new type of surface gray matter, the neopallium or neocortex. This may develop to some slight degree in reptiles; in mammals the neopallium takes over the greater part of the expanded and generally highly convoluted surface of the hemispheres. This new covering is from the first a highly developed type of association center, with four to six layers of cells present throughout its extent. It receives, like the basal nuclei, fibers which relay to it sensory stimuli from the brain stem. As it has developed in mammalian evolution it has come to take over all the higher mental functions present in either the tectum or the basal nuclei in other groups and has become not only the major directive center of the animal's activities but the seat of memory and of such qualities of "intelligence" and "consciousness" as may be attributed to the mammalian organism. Other, older centers, such as the tectum and basal nuclei, usually exercise control over muscular activity through various relays; the mammalian neopallium has developed a powerful pyramidal tract of fibers which extends directly from the cortex to "voluntary" motor regions of stem and cord.

With expansion, the neopallium of the hemispheres tends to cover and envelop other brain structures in more progressive mammals, as may be seen by comparing more primitive mammalian brains such as those of Figures 382, C; 385, B; and 387, C, with Figures 383, B; 385, B; and 388, B; in this process there is much shifting and distortion of older hemisphere areas and a complex build of the enclosed ventricles, as may be seen in Figure 397. Since the neopallium is essentially a sheet rather than a solid mass of material, simple increase in size of the hemispheres would be an unsatisfactory means of growth, and in advanced mammalian types the cortex is highly convoluted and thrown into folds or grif, with intervening furrows, the sulci.

The mammalian cortex is often described as composed of frontal, parietal, occipital and temporal lobes. These terms, however, are merely topographic and have no precise meaning as regards the architecture or functioning of cortical areas. There is a complex "wiring" system connecting all parts of the cortex with one another, suggesting that the gray matter is essentially a unit, equipoten-

tial in all its parts for any cerebral activity. Experiments on laboratory animals and study of the results of disease or injury on human brains show that this is true to a considerable extent. On the other hand, it is clear that certain cortical areas are normally associated with specific functions (Fig. 398). The front part of the neopallium includes a motor area; the posterior part is associated with sensory perception, special regions are associated with eye and ear; in a general "somatic sensory" region are definite areas for reception of skin and proprioceptive sensations from various specific parts of the body. In man particularly, however, we find that these specific functional areas of the neopallium occupy only a relatively small part of the surface. Between them are found large "blank areas" of gray matter, most conspicuously one occupying much of the frontal lobe. Obviously these regions are far from blank; they are association areas of the highest and most generalized type, the seat of such mental properties as learning ability, initiative, foresisht and indement.

Brain Patterns—Summary. We may summarize here some of the main features of brain structure described in brief fashion above.

Much of the brain stem is a persistently primitive region, with motor and sensory columns and centers rather closely comparable to those of the spinal cord. The history of brain evolution has been mainly one of the development, above and in front of the medulla, of higher centers; most prominent of such centers are dorsal outgrowths of huminated gray matter which have grown up in areas concerned with the three special senses. In such centers sensory data are assembled and synthesized and resultant motor stimuli sent out to the motor areas of brain stem and cord.

1. The primary center of reception for equilibrium and lateral line stimulies in the medulla; above this developed the cerebellum, which initiates no bodily movement, apart from posture reflexes, but insures that motor directives initiated in other centers be carried out in proper fashion. The principal "information" upon which it acts comes from the adjacent ear and lateral line centers and the proprioceptive system of the muscles and tendous. In mammals intimate connections are established between cerebellum and cerebral hemispheres.

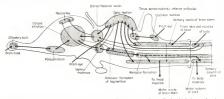


Fig. 599. Diagram of the main centers and "siring" arrangement of a reptile, in which the tetal region of the milliam jays a dominant role the corpus triatual modes angulai to a some importance are relation center, but the necourtex (necessition) is unimportant. The retrivalar formation of the bram store (ross batched) is important in carrying most implies to mote in the store and cord. In this overinghic field singram only a limited number of gaths between somatic receptors and effectors are included; usceral center and paths are omitted, as are certellar connections shown in Fig. 300, p. 394).

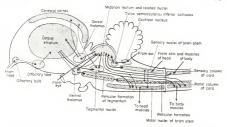


Fig. 400. A "wiring diagram" of a bird brain, comparable to that of Figure 399. The midbrain tectum is still of importance, but the corpus striatum is the dominant center in many regards.

2. In lower vertebrates the main centers dominating nervous activity are situated in the brain stem. (a) A great center of coordination and of initiation of motor activity is established in the midbrain tectum (Fig. 39); this is primarily a visual center, but to it are relayed stimuli of all other somatic sensory types, and from it are sent out directives to the motor centers and columns. As we ascend the vertebrate scale the tectal region becomes rivalled and then exceeded by the hemispheres, and in mammals the tectum is of small importance. (b) The tectum is somatic in nature; corresponding centers for visceral sensations and visceral motor responses are established in the hypothalamus.

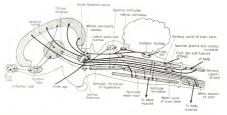


Fig. 101. A "wiring diagram" of a mammalian brain comparable to Figures 399 and 400. The midbrain tectum is reduced to a minor refex center, and the corpus striatum is relatively unimportant; most sensory impulses are projected "upward" to the cerebral cortex, whence a direct motor path (pyramidal tract) extends to the motor centers of brain stem and cord.

3. In higher vertebrates the cerebral hemispheres, originally only a center for olfactory sensation, have become more and more important as association centers. (a) First of cerebral areas to gain importance is that of the basal nuclei or corpus striatum, to which in all amniotes tracts from the thalamus relay somatic sensations and from which return fibers carry motor stimuli to middrain and motor columns. In reptiles the corpus striatum rivals the older tectum in importance and in birds it is a dominant center (Fig. 400). (b) In mammals, however, a different development has occurred (Fig. 401). In the gray matter of the cortex there develops a new, greatly expanded correlation and association center, the neopallium. This assumes the greater part of the higher functions once concentrated in the tectum or corpus striatum, gains a complete array of somatic sensory data through projection fibers from the thalamus, and develops direct motor paths to the motor columns of the brain stem and spinal cord.

# 17

## ENDOCRINE ORGANS

In the last chapter we described, in the nervous system, an exceedingly complicated but highly efficient method of coordinating bodily activities by "messages" received from and sent to specific areas of the body with speed and precision. We shall here consider a second integrative system, under which information and directives are carried through the blood by chemical "messengers," the homones produced by endocrine glands. This method transmission is, of course, slower than transmission by nerve impulse, and homonal effects are often broadly distributed over the body to a variety of organs and tissues, in contrast to the "pinpointing" possible in the nervous system. But despite the seeming irrationality and vagueness of hormonal transmission, many of the hormones are not only important but are absolutely essential for the maintenance of the life of the organism.

For convenience, I have gathered in this chapter data on all the known homone-producing structures of the body, although they do not form an organ system, but are scattered here and there throughout the body—in some cases literally from stem to stem—and may derive from a variety of sources. The situation is somewhat similar to that of hemopoletic organs; just as it makes no difference in which part of the body blood corpuscles are produced, so too the area in which hormones are produced is inconsequential, as long as they can be passed into some element of the circulatory system and thence be distributed throughout the body.

Neural and hormonal systems of communication, although distinct, are far from independent of one another. Directly or indirectly, the nervous system may be powerfully affected by hormones. On the other hand, the "master gland" of the endocrine system, the hypophysis, is strongly influenced by the adjacent hypohalamus, and some of its hormones are actually produced by ganglia in that brain region. Again, the adrenal medulla, although an endocrine organ, is composed of modified nerve cells.

Which is the older regulatory system, nervous or endocrine? There is no clear answer to this; probably they evolved in parallel fashion. Elementary nervous systems are present in the most primitive metazoan animals. Hormonal systems are known in numerous invertebrates, and undoubtedly many more await discovery. Any chemical material given of fby a cell as a result of its metabolic processes is liable to have some effect, favorable or deleterious, on other parts of the organism. There quite surely went on, in the course of the rise of chordates, processes of evolutionary selection of chemical products favoring the survival and well-being of the organism—processes quite comparable in nature to those under which morphological structures were evolved.

#### THE HYPOPHYSIS

Below the diencephalic region of the brain lies a small but most essential structure, the major endocrine organ of the body, the pituitary gland or hypophysis cerebri (Figs. 209, p. 232; 381–385, pp. 388–391; 402; 403). In most vertebrates the pituitary tissues form a single compact mass, contained in a pocket the sella turcicaj in the floor of the braincase. Actually, however, the gland is a dual structure, its two portions having very different embryological origins and functionize in different fashions (Fig. 404).

Downward from the embryonic diencephalon extends a hollow, finger-like process, the infundibulum. Upward from the embryonic mouth there grows an ectodermal pocket, the hypophyseal pouch (Rathke's pouch). From both these embryonic structures there proliferate masses of tissues, which unite to form the

adult pituitary, or hypophysis.

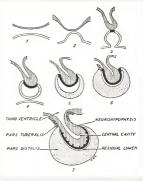
Although various 'terminologies have been applied to subdivisions of the pland, it is best considered as consisting of two parts or lobes in accordance with its embryonic origins: the adenohypophysis, derived from the hypophyseal pouch, and the neurohypophysis, formed from brain tissue. The major portion of the adenohypophysis—in fact, the major portion of the whole gland—is the pars distalis. In addition there may be distinguished, particularly in mammals, a pars intermedia, which may tuse with the neural part of the gland. The neurohypophysis consists mainly of the lobus nerrosus, or neural lobe; but the infundibulum, from the bottom of which the lobe develops, may also be considered as part of



Fig. 402. Section through a human pituitary and the adjacent structures at the base of the brain. (From

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Fig. 403. Diagrams showing stages in the development of the mammalian pitultary from brain tissue (hatched) and from the ix-pophyseal (Rathke's) pouch. As wall be seen, only the neurohyophysis is formed from neural material; the three other parts, constituting the adenohyophysis, are derived from the pouch epithelum, (Mer Turner.)



the neurohypophysis. And as we shall see, a fraction of the hypothalamus is functionally also a part of the neurohypophyseal apparatus.

There is considerable variation in pituitary structure among some of the lower vertebrates. In the lamprey, for example, there is no formed neural lobe, its homologue being simply a plate of tissue in the floor of the diencephalon, and the adenohypophysis is formed of tissue derived from a tube leading backward beneath the brain from the nostril opening (Fig. 231, B., p. 247). In caritlaginous fishes, there is found a distinct infundibulum and a well-formed mass of neural lobe tissue. Here, and in almost all higher types, the hypophyseal pouch is closed and there is a well-developed adenohypophysis, but in shark-like fishes and ray-finned types there are no well-marked subdivisions of that part of the gland. In lungishes and in a majority of land animals there is a distinct pars intermedia in addition to the pars distalis; but a pars tuberalis is a relatively uncommon development.

It was originally assumed that the hormones given off by both parts of the hypophysis were produced by the cells located in the organ itself. In recent years, however, it has been discovered that the neural lobe is merely a storage area for the hormones that it passes into the blood. The hormones are actually formed in the cell bodies of brain neurones of the nervous system, located in nuclei of the hypothalamus that are termed the supraoptic and paraventricular nuclei. The materials secreted by these cells pass down their axons into the neural lobe for storage and eventual entry into the blood.

In contrast, the more numerous hormones of the adenohypophysis, both pars distalis and pars intermedia, are produced by the cell masses actually present in

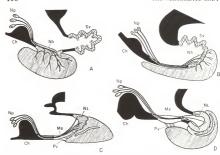


Fig. 404. Median sagittal sections of the pituitary of A, the teleost Anguilla: R, the shark S-yllordning, the lumph frapropersus B, an aminisch. Advendopopolysis, fine latchings mendropopolysis sipple. Δο, Optic chiasma; Me, median eminence: Wa, neurolopopolysis: W, formed neural lolte: V<sub>b</sub>, prospite neuronecrectory uncelle; Pr. portal vesselse S, vs. saccus vs.cesious. To show sepeculity the neurones yaught to the neurolopopolysis and the portal system of lumglesh and tetrapods. (From Wingstrand in Cordman, Comparative Endocrinolopes, John Wiles and South

these structures. The adenohypophysis is strongly influenced in its hormone production by the brain. The means by which this influence is exerted is a matter of interest. In many fishes nerve fibers pass into the adenohypophysis, thus affording a reasonable path by which the brain can affect glandular activity there. But lungfish and tetrapods this is not the case. Nerve fibers may enter the pars intermedia, but (except for some which appear to be autonomic fibers for blood vessels) none penetrate to the pars distalis, where almost all the hormones are formed. In this condition, how does the brain influence the gland?

Apparently indirectly, through a curious local portal system of tiny blood vessels. The vissels supplying arterial blood to the adenohypothysis pass close to or through the floor of the diencephalon anterior to the infundibulum. A tract carrying secretions to the neural lobe passes through this same area, which particularly in mammals tends to form a bit of a swelling on the lower surface of the brain, termed the median eminence. In lungfishes and tetrapods the blood vessels to the adenohypophysis enter the region of the median eminence, break up into a capillary system, then re-collect as a set of small portal veins to pass on to the pars distalis. It is thought that in passage through the median eminence the blood picks up neurohumoral materials that act as agents transmitting "information" from the brain to the gland. This seems a curiously roundabout up of accomplishing an important function, but no other effective method is known or has been suggested.

Attempts have been made to identify predecessors of the hypophysis, or of its components, in lower chordates. Amphioxus has small pits in the roof of the

mouth and the floor of the brain tube above, which have been compared to the hypophyscal pouch and infindibulum respectively, but the homology is very uncertain. In adult tunicates there is present a neural gland, which is in certain regards suggestive of a pituitary (Fig. 16). This gland opens into the morphologically dorsal side of the entrance to the pharynx, and lies close below the ganglion which is the nearest approach to a brain structure present in the simple nervous system of the adult tunicate. Morphologically, the neural gland could reasonably be considered as antecedent to the hypophysis, but there is at present no positive evidence that it is an endocrine producing structure.

Some nine or ten hormones are known to be produced by the pituitary. Still others have been, or are, suspected to be present in that gland. The greater part of the work concerned with hormones has been done on the mammalian pituitary, but a large part of the whole series is found throughout the vertebrate classes. Most pituitary hormones are produced by the adenohypophysis, principally by the pars distalis. All are proteins or polypeptides. They may be listed and briefly described:

GROWTH HORMONE or SOMATOTROPHIN (STH) has a very broad influence on growth and metabolism in general, with marked influence on growth of skeleton and muscle, metabolism of fats and earbohydrates, and retention of protein nitrogen in the tissues; it further acts to enhance the effect of other hormones on the activity of thyroid, adrenal cortex, and reproductive organs.

CORTICOTROPHIN (ACTH) is vital for adrenal cortex activity in secretion of hormones and exerts some metabolic influence in other regards.

Thyrotrophin (TSH) is essential for the stimulation of the thyroid to form and release thyroid hormones.

Productive is mainly associated with sexual structures and activities and hence with the next two hormones is termed gonadotrophic. These hormones are best known (and named) from their observed effects in mammals. Prolactin stimulates milk secretion and prolongs the functional life of the corpus lutem (and consequent continued secretion of progesterone; cf. p. 418). We know little of its function in other vertebrate classes except for such observations as its stimulating the crop gland for feeding the young in pigeons, and stimulating newts to enter the water for reproductive purposes.

LUTINIZING or INTERSITIAL CELL-STIMULATING HORMORE (LH or ICSH) influences maturation of the gonads and production of sex hormones; acts in formation of the corpora lutea and secretion of progesterone in the ovary; and stimulates the interstitial cells of the testis, promoting the production of male sex hormones and the maturation of sperm.

FOLLICLE-STIMULATING HORMONE (FSH) stimulates the growth of ovarian follicles and, in conjunction with the luteinizing hormone, promotes female sex hormone secretion and ovulation; it may possibly promote spermatogenesis.

INTERMEDIN, or MELANOCYTE-STIMULATING HORMONE (MSH) acts to disperse pigment granules in melanophores and darkens the skin. In contrast to the hormones listed so far, this one (as its name indicates) is produced by the intermediate portion of the gland when this part is distinctly developed.

Melanophore-Concentrating Hormone (MCH) acts in opposition to intermedin and causes contraction of melanophore pigment granules; is found in fishes and amphibians but not, apparently, in amniotes.

In contrast to the wealth of hormones produced by the adenohypophysis, the secretions given off by the neurohypophysis are only two in number: the polypep-

tides rasopressin, or antidiuretic hormone (ADH), and oxytocin. Vasopressin is principally associated with increasing blood pressure through contraction of arterioles and controlling water output or intake in various fashions in the different vertebrate forms. Oxytocin is best known from its effects on the female mammal in promoting contraction of uterine muscle, and development of the mammary gland and ejection of milk after the birth of young; it appears, however, that this hormone has sexual effects on at least certain other vertebrates, as, for example, spawning in minnows. It seems clear that, in contrast to the importance of the numerous hormones of the adenohypophysis, those of the neural lobe play a relatively modest part in the body economy and are not indispensable.

#### PARATHYROID GLANDS

Among the glands derived in tetrapods from the gill pouch region of the embryo are small structures, usually two pairs, termed the parathyroid glands (Figs. 245, 246, 247, p. 258; 405). In the adult these are situated at somewhat variable positions in the neck region. In man, they are embedded in the thyroid tissues. Attention was long ago called to these glands through the discovery that extirpating parts of the human thyroid containing them resulted in the death of the patient, this because, as is now known, the parathyroids are deeply involved in the metabolism of calcium and phosphorus. Parathyroid

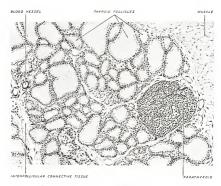


Fig. 405. Thyroid and parathyroid tissues of the rat. (From Turner.)

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glands as such are absent in fishes, but there is evidence to suggest that the ultimobranchial bodies, budded from the back end of the gill pouch series, are related in some degree, at least, to calcium metabolism.

#### THYROID GLAND

Also derived from the throat, but (in contrast to the parathyroid) budded from the floor of the embry opharynx rather than its walls, is the thyroid gland (Fig. 405). In adult fishes it is situated below the gill chamber, and in tetrapods, generally ventral to the windpipe at some point along the length of the neck. In a majority of vertebrates it is a single structure, although often bilobed; in birds, amphibians and teleoats it is typically paired in the adult. In teleoats, and to a lesser extent in other vertebrate types, small detached masses of thyroid tissue may be found in places far removed from the main gland. The thyroid tissue most of the properties of an iodine-bearing protein from which the iodine-bearing hormones are formed and discharged into the blood. The thyroid products are highly important in maintaining tissue metabolism, and are concerned with reproductive functions and growth phenomena. Most spectacular of the thyroid functions is control of metamorphosis in amphibians.

The thyroid has a pedigree that stretches far back in chordate history. In both Amphiovas and tunicates there are present ciliated and partly glandular channels along which food particles strained out of the water current are carried back to the intestinal region (Figs. 4-6, pp. 15, 16, 18). Such a channel in the floor of the pharynx of Amphioxus is that termed the endostyle. In both Amphioxus and tunicate endostyles there are produced iodine compounds that are carried on into the digestive tract together with food materials. Ammoocetes larva of lampreys have a similar feeding habit and ciliated grooves much like those of Amphioxus and tunicates. Here the ventral groove terminates posteriorly in a deep pouch in the pharyngeal floor, where there is produced an iodine-bearing material that is carried on down the diagestive tract (Fig. 231, 4, p. 247).

The endostyle, including the Ammocoetes gland, is a median ventral pharyngeal structure, comparable in position to the thyroid gland. Are they truly homologous? The lamprey gives us a positive, conclusive answer. At metamorphosis the larval endostyle pouch closes off from the gut and breaks up into a series of follicles that are indisputably thyroid in structure. The thyroid, it would seem, was originally an exocrine gland, whose products were taken into the digestive tract. It has become an endocrine organ; but it is of interest that, alone of hormones, those of the thyroid can still be taken by mouth.

#### PANCREATIC ISLANDS

Although the greater part of the glandular tissue of the pancreas is devoted to the production of enzymes that pass through ducts to the intestine, areas of tissue of another type can be seen distributed through the gland as isolated islands (Fig. 263). These "islets of Langerhams" consist of cells glandular in nature, but no furnished with ducts; they thus obviously form an endocrine organ, sending

secretions into the blood. The insular material is usually diffused among the ordinary tissues of the formed pancreas. In teleosts, however, small clusters of islet cells are spread here and there in the general gut region, and in a few fishes these tissues make up a small special organ of their own.

The islands produce a specific protein hormone, insulin. This material has an important regulatory action on metabolism, particularly of carbohydrates; interruption of its supply brings on the disease diabetes mellitus. A second substance, the polypeptide glucagon, is also produced in the pancreatic islands; this tends to increase blood sugar but he breaking down of glycogen in liver storage.

#### INTERRENAL TISSUES AND THE ADRENAL CORTEX

In most tetrapods there is found, adjacent to the kidneys and capping them, a pair of endocrine structures termed the adrenal glands (or epinephric glands, Figs. 273, 275). Microscopic examination shows the presence in them of two different types of tissues, intermingled or juxtaposed in lower tetrapods, but formed into distinct cortical and medulary layers of a single compact organ in mammals (Fig. 406). Both parts are endocrine glands, but of very different sorts. The metulary tissue is a modified part of the nervous system (discussed later, pp. 445–446). The cortical substance is of quite another nature. Fishes almost never have formed adrenals, but in sharks the two components are quite distinct. In other fishes diffuse cell masser representing both components can be found be-

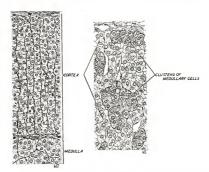


Fig. 406. A section through part of the adrenal gland (outer surface above) in a mammal (rat), with division into cortical and medullary layers, and a reptile (Heloderma), in which the two tissues are intermigled. (From Tumer.)

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tween and around the kidneys and along the course of the major blood vessels dorsal to the celom. The cortical materials are termed interrenal tissues.

That the cortical material is vital for the maintenance of life was recognized more than a century ago, for human deaths from an ailment known as Addison's disease were invariably associated with deterioration of the adrenal cortex. The cortex cells have since been discovered to secrete a series of steroid hormones, which have widespread influence over bodily functions. The broad functions of the cortical hormones lie in aiding the body to meet long-continued environmental stresses, in contrast to the function of the adrenal medulla in coping with brief emergencies (as discussed below). More specific effects of the cortical hormones are, among others, on regulation of the salt and water balance in cells and body fluids, and on metabolism, particularly of carbohydrates.

The importance of cortex hormones in water and salf regulation suggests a relationship of some sort between the cortical materials and the kidneys. That this physiologic association and the close physical relationship of kidney and adrenal are not accidental, but have historic significance, is indicated by the embryologic origin of the cortical tissues. They appear as strands of cells, which bud off from the epithelium of the roof of the celom medial to the developing kidney tubules and lateral to the gonads. Kidney and adrenal cortex are thus derived from adjacent regions of the embryonic mesoderm.

#### CHROMAFFIN TISSUES AND THE ADRENAL MEDULLA

Very different in origin and function from the cortical portion of the adrenal gland is its medullary portion and the structures antecedent to it in lower vertebrates. Here we are dealing with a portion of the nervous system which has been modified to perform an endocrine function. We have seen that the visceral motor nerve supply to the internal organs of the body is of a peculiar type in which the impulses do not directly reach the smooth muscles or glands concerned, but are relayed through a scries of postganglionic neurons, which give off neurorhumors at their tips. The cells of the adrenal medulla and homologous structures in lower vertebrates are much modified postganglionic neurons.

In various instances there are described clusters of cells found throughout the vertebrate body, particularly along the region near the dorsal aorta or adiacent to sympathetic ganglia, which are termed chromaffin cells. The name is derived from the readiness with which they are stained by certain potassium salts. Embryologically, they arise from cells migrating downward along the path of the visceral nerve rami, and are thus identical in origin with the postganglionic neurons of the sympathetic system. In fishes, small masses of such cells, often associated with interrenal tissues, are present between the kidneys and along the dorsal wall of the body cavity. They are appropriately termed paraganglia, since they are embryologically identical with the sympathetic ganglia, which they may adjoin, particularly in sharks (Fig. 373). In tetrapods occasional small cell clusters of this type persist, but most of the chromaffin material is concentrated into a compact mass of tissue, which forms part of the adrenal gland capping the kidney. In mammals the chromaffin cells are concentrated in the center of the adrenal body, forming its medulla (Fig. 406); in lower tetrapods they are more diffuse and interspersed with the cortical component.

These cell masses are innervated by autonomic nerve fibers, commonly pre-

ganglionic; on stimulation they secrete into the blood two related chemicals, which are identical with those given off by the postganglionic fibers of the sympathetic system: adrenalin and nonadrenalin. Here, however, adrenalin is the more abundant product. The cells of the adrenal medulla do not look like nerve cells, for they lack any fiber processes. But since they are homologous with postganglionic sympathetic neurons, it is not surprising that they produce comparable neurohumors. The contrast is that the true postganglionic sympathetic cell produces only a tiny amonat of adrenalin-like material, which affects only structures immediately adjacent to it, whereas the mass of adrenal cells is capable of rapidly releasing large quantities of these materials, which may have a strong, immediate, "shotgun" effect on all parts of the body when carried about by the circulatory system. "bracine" the organism to meet emerencies.

#### UROHYPOPHYSIS

Just as in all vertebrates a special anterior secretory area of the central nervous system may develop as the neurohyophysis, so in most, if not all, fishes a posterior secretory system may arise. To this system (not unreasonably) the term undryophysis has been given. This is highly developed in many telesots (Fig. 407). In the nerve cord, toward the end of the tail region, can be found large cells, obviously secretory in nature. Fibers—axons—extend backward from these cells and may terminate in bulbous tips, which are filled with secreted material. These bulbs are most commonly clustered together on the underside of the cord, causing a slight swelling or a wart-like structure, often readily visible to the naked eye upon dissection. The nature of the secretion is as yet imperfectly known, but it appears to influence regulation of the salt content of the bodo, and in teleosts appears to affect the secretion of gas into the swim bladder.

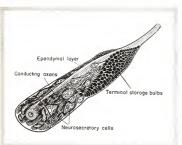


Fig. 407. Urohypophysis of an eel. The end of the spinal cod is seen as if transparent (except for the inner, ependymal lawer of cells). Visible are a number of secretory neurons, the axons along which the secretion flows, and the swollen bulbs at the ends of the axons. (After Enami, in Gorbman, Comparative Endocrinology, John Wiley and Sons.)

#### SEX HORMONES

Far more than any other activity, reproduction in vertebrates is powerfully influenced by hormones, with regard to both anatomical structures and behavior patterns. The subject merits a volume in itself, here we will but briefly not be aspects of this complex picture that are of morphological significance. The sex hormones, as noted earlier in this chapter, are strongly influenced by the gonadotrophic hormones of the pituitary,

With one exception,\* the hormones produced by the gonads are steroids, termed autrogens when produced primarily by the testis, and estrogens when produced by the ovary. These steroids are very similar in chemical composition to the hormones of the adrenal cortex. The relationships are in fact so close that the gonads and cortex are, as it were, unable to completely sort out their respective roles as hormone producers. A limited amount of sex hormones may be detected among the cortical secretions, and a small fraction of the gonadal hormone products are substances proper to the adrenal cortex. Still further, male and female gonads are not completely differentiated in their products, for the male gonads are found to secrete a certain amount of female hormone, and vice versa.

This similarity of hormone products between adrenal cortex and gonads correlates with the similarity in origin of the cells that produce them. Apart from the actual sex cells (which are not involved in hormone production), all the materials making up the gonads are derived, we have seen, from the mesoderm lining the dorsal rim of the celonic cavity on either side of the middine, and the cortical adrenal cells are derived from the adjacent region of the mesoderm, between gonad and kidney (p. 292).

The major androgen of the male gonad, where analysis has been made, is the steroid testosterone; in the female the major steroids are the estrogens, estradiol and the much less potent estrone. What cellular elements in the gonads produce these sex hormones? The major source in the testis appears to be distinctive interstitial cells, which are quite separate from the formed seminiferous tubules or ampullae and lie (together with connective tissue) in the interstices between them (Fig. 286). In certain cases, however, a second source of androgens appears to be present. In the lining of the tubules or ampullae there are found, beside the sperm-producing elements, supporting cells (Sertoli cells) that have the same embryonic origin as the interstitial cells and may have similar hormone-producing potentialities (Fig. 286). Ovarian cellular materials are of common embryonic origin with interstitial cells and there may be a certain amount of interstitial tissue in the ovary. Most ovarian cells, however, are engaged as follicle cells, furnishing sustenance to the developing eggs. In addition to this function, the follicle cells are the major producers of estrogens, although minor amounts of interstitial tissues present may also be concerned in this process (cf. p. 294, Fig. 285)

Apart from the production of the primary sex hormones, we find that in the ovary a second type of steroid hormone formation may occur. When an egg bursts from the ovary, one would expect the follicle in which it has been enclosed to degenerate. This appears to be the case in many groups; but in mammals, most outably, there is no immediate degeneration. Instead, the follicle cells long per-

<sup>\*</sup> The exception is the protein relaxin, a female hormone that relaxes the pelvic symphysis and facilitates birth of offspring in mammals and also has functions aiding reproduction in lower vertebrates.

sist, forming a yellow-colored material, the corpus luteum, and filling the empty follicle. The corpus luteum cells in mammals secrete an important steroid hormone, progesterone; this prepares the uterine epithelium for implantation of the ovum and, if fertilization and implantation are accomplished, stimulates the development of a placenta. But although major interest in the corpus luteum and its hormonal function has been centered on mammals, with their placental type of development, it is found that a corpus luteum (likewise apparently productive of progesterone) develops after the bursting of the egg follicle in elasmobranchs. Still further, although no typical corpus luteum is formed in other vertebrate groups, progesterone has nevertheless been discovered in the ovaries of certain other vertebrate types, including birds. A small percentage of elasmobranchs and a few lower tetrapods bear their young alive, but in general no major specific function is known for progesterone in lower vertebrates. This suggests that we have in progesterone an example of the process of hormonal evolution proposed at the beginning of this chapter, that of a chemical product given off by a tissue that originally had little positive function, but later came to serve a useful role in the economy of the body and in mammals has at last become an important hormone

The nature and functions of the mammalian placenta are part of the story of vertebrate embryology rather than vertebrate anatomy. We may, however, note here that during the course of pregnancy, the mammalian placenta itself becomes an endocrine-producing organ, secreting a number of steroids, including not only esteroids and propersterone but also a special gonadotropic hormone of its own, which is important in maintaining pregnancy.

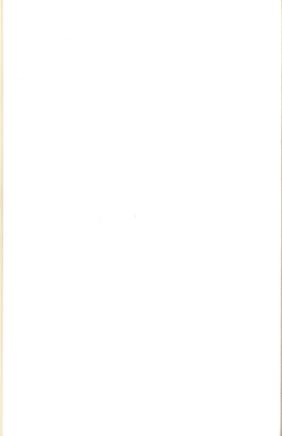
#### OTHER HORMONES

Hormones so far discussed have been produced by specific endocrine glands and in general form an interlocking system, acting with and against one another. In contrast to this is a series of gastrointestinal hormones, produced from the ordinary gut epithelium and "independent" of other hormones in their production and action. It is thought that the mucosa of the pyloric region of the mammalian stomach produces a hormone, gastrin, which affects the secretion of hydrochloric acid in the fundas region. More definitely proved is the production of secretin by the proximal portion of the small intestine when flood enters this region of the gut; this stimulates the flow of pancreatic juice. There is evidence of a second intestinal hormone that stimulates pancreatic secretion; and a further intestinal endocrine product, cholecystokinin, effects evacuation of the gallbladder when fats enter the intestine. Still further hormonal agents may be produced by the gut epithelium and aid in regulation of activities along successive sections of the dieseive tube.

In other areas of bodily activity there are evidences of influences caused by chemical materials carried through the blood. In most such cases, however, there is little evidence of production of such chemicals by specific "endocrine" structures and it is difficult to know where to draw a line.

There are a number of body structures whose tissues have a glandular appearance and hence have been suspected, despite the absence of convincing evidence, of having endocrine properties. Most often cited in this category are the pineal and parapineal structures, which tend to persist even when their original ENDOCRINE ORGANS 419

visual function has been lost (as in the mammalian pineal organ). Now and again observations have been made of bodily changes consequent on removal or disease of the mammalian pineal, or effects on the pineal following such operations as castration. But the results are far from clear, and recent hypotheses as to pineal function have little more to support them than Descartes' suggestion, centuries ago, that the pineal is the seat of the soul. We have noted earlier that the functions of the thymus are not too well known; endocrine activity has been suggested but not demonstrated. Again, ultimobranchial bodies, budded off from the last gill pouch, have been thought to have some possible hormonal nature, and we have noted some suggestion that a fish ultimobranchial gland may function after the fashion of a parathyroid. However, small ultimobranchial structures are present in tetrapods, which have true parathyroids as well; their function here is quite unknown.



# A SYNOPTIC CLASSIFICATION OF CHORDATES

The classification given here is presented primarily for the purpose of allowing the student to place in their proper position the forms discussed in the text. In consequence, no attempt is made to list the genera of vertebrates, and in many cases families, suborders, and even orders are neglected when such subdivisions of groups lack interest for present purposes. To fill out the picture, the more important fossil forms are mentioned, although our anatomic knowledge of them is practically confined to the skeletal system.

In addition to the major terms in the classification given below, (1) the first three subphyla are often termed Protochordate, lower chordates, in contrast to the Verebrate, (2) among the vertebrates, the term Gnathostomata, jawed vertebrates, may be used to contrast all other higher vertebrate groups with the class Agnatha; (3) Terapoda is Trequently used for amphibian and higher four-footed types in contrast with Pisces, fishes in a broad sense; (4) Anniola, referring to features of embryonic development found in repitles, birds, and mammals, may be used for these three classes, all fishes and the amphibians as well being grouped as Anamiota.

#### PHYLUM CHORDATA

#### SUBPHYLUM HEMICHORDATA

(Little or no development of notochord or dorsal nerve cord. Often considered as constituting a separate phylum, distinct from the Chordata, although closely related)

#### Class Pterobranchia

(Simple, Sessile, Plantlike Animals, Gathering Food by Ciliated Lophophores) (Fig. 8, A, B, p. 20)

# Class Enteropneusta

(Worm-shaped Burrowers, with Well Developed Gill Apparatus. The Acorn Worms) (Figs. 8, F; 9)

#### SUBPHYLUM UROCHORDATA

(The tunicates, with notochord and nerve cord well developed in larvae in many cases, but adults sessile or floating organisms, mainly consisting of an elaborate gill apparatus) (Figs. 6, 7, 8, C-E)

# SUBPHYLUM CEPHALOCHORDATA

(Amphioxus, with notochord, nerve cord, and gill apparatus all well developed in the adult stage) (Fig. 4, p. 15)

# SUBPHYLUM VERTEBRATA

(Generally with developed backbone and with other advanced structures in skeleton, brain, kidneys, etc., characteristic of true vertebrates)

# Class Agnatha

(Jawless Vertebrates)

- Orders Osteostraci, Anaspida, Heterostraci. These constitute the ostracoderms of the Silurian and Devonian periods. Representatives of these three groups are shown in Figure 18 (p. 38). Cephalaspis-like forms of the Osteostraci are also shown in Figures 19 and 232 (pp. 38, 248).
  - Order Cyclostomata. The living cyclostomes (Figs. 16, 17, pp. 36, 37).

SUBORDER MYXINOIDEA. Hagfishes.

Suborder Petromyzontia. Lampreys.

#### Class Placodermi

(Primitive Jawed Vertebrates; Extinct and Confined to the Paleozoic)

Order Acanthodii. Spiny "sharks" (Fig. 20, A, p. 40).

Order Arthrodira. The arthrodires; jointed-necked fishes (Fig. 20, B).

Order Antiarchi. Related to arthrodires, but with peculiar bony "arms" (Fig. 20, C).

Order Macropetalichthyida.

Order Stegoselachii. The last two orders are modified arthrodire relatives which are suspected of being transitional, with reduction of bony armor, to the sharklike fishes.

# Class Chondrichthyes (Cartilaginous Fishes)

SUBCLASS ELASMOBRANCHII (Sharks and Related Forms)

Order Cladoselachii. Primitive Paleozoic sharks (Fig. 22, A, p. 42).

Order Selachii. Typical sharks, Paleozoic to Recent, with claspers, narrow-based fins, and so forth (Fig. 22, B).

Order Batoidea. The skates and rays (Fig. 23, p. 43).

SUBCLASS HOLOCEPHALI (Differing from Sharks in Having an Operculum, Upper Jaws Fused to Skull, and so on)

Order Bradyodonti. Paleozoic forms, poorly known, mainly represented by tooth plates.

Order Chimaerae. The chimaeras (Fig. 22, C).

#### Class Osteichthyes

(The Higher Bony Fishes) (see Fig. 25)

SUBCLASS ACTINOPTERYGII (Ray-Finned Fishes)

Superorder Chondrostei. Primitive ray-finned fishes, with heterocercal tails, and so forth, represented by fossil palaeoniscoids (Fig. 29, A, p. 49), mainly Paleozoic, and three modern types: Polypetrus (Fig. 29, B), the sturgeons (Fig. 30, B, p. 50), and the paddlefish (Fig. 30, A).

Superorder Holostei. Dominant ray-finned forms of the Mesozoic, with abbreviate heterocercal tails, and so on; living forms include the gar pike and Amia (Fig. 31, p. 51).

Superorder Teleostei. The dominant fishes of Cenozoic and Recent times, with a homocercal tail. Include many thousands of forms, classed in a number of orders (Fig. 33, 34, pp. 53, 54).

SUBCLASS SARCOPTERYGII (CHOANICHTHYES) (With Fleshy Fins)

Order Crossopterygii. Forms broadly ancestral to land vertebrates. Mainly Paleozoic fossils; one aberrant living form (Fig. 27, p. 47).

Order Dipnoi. The lungfishes, including three living genera. Many similarities to ancestral types, but aberrant in teeth, skulls, and so forth (Fig. 28, p. 48).

# Class Amphibia

(Tetrapods, but without Development of Amniote Type of Egg)

SUBCLASS APSIDOSPONDYLI (Amphibians in Which Vertebral Centra Were Primitively Formed by Pleurocentra and Intercentra [cf. Figs. 104, 105, pp. 138, 139])

Superorder Labyrinthodontia. The stem Amphibia, extinct, but dominant in late Paleozoic and Triassic times. Includes many dozens of fossil genera arranged in several orders.

Superorder Salientia, Order Anura. (Subclass position uncertain) The frogs and toads; living forms have highly specialized limbs and shortened trunks, and so on. Pleurocentra and intercentra reduced or absent.

SUBCLASS LEPOSPONDYLI (Vertebral Centra Formed as Single Structures, often Spool-shaped)

Orders Aistopoda, Nectridia, Microsauria. These are late Paleozoic fossils: the last consists of small forms from which the two living orders may have descended.

Order Urodela. The salamanders and newts, with a normal body form. but many degenerate characters.

Order Apoda (or Gymnophiona). Wormlike, burrowing types,

# Class Reptilia

(Amniotes, but without Advanced Avian or Mammalian Characters [cf. Fig. 37, p. 59])

SUBCLASS ANAPSIDA (Without a Temporal Opening)

Order Cotylosauria. Archaic "stem reptiles" of the late Paleozoic and Triassic.

Order Chelonia (Testudinata). The turtles.

SUBCLASS SYNAPTOSAURIA (Extinct Groups, Characterized by a Single Temporal Opening High Up on the Side of the Cheek)

Order Protorosauria. Includes various obscure Permian and Mesozoic reptiles.

Order Sauropterygia. The plesiosaurs and their relatives; marine Mesozoic reptiles swimming by means of limbs transformed into powerful paddles.

SUBCLASS ICHTHYOPTERYGIA

Order Ichthyosauria. The ichthyosaurs, with a body highly specialized for marine life

SUBCLASS LEPIDOSAURIA (Diapsid Type of Temporal Region; without Archosaur Specializations) Order Eosuchia. Permian and Triassic ancestral diapsids. Order Rhynchocephalia. The living Sphenodon of New Zealand and

fossil relatives. Order Squamata. Lizards and snakes. Related to the last, but temporal

arches reduced SUBCLASS ARCHOSAURIA (Ruling Reptiles. Diapsid Temporal Region, with Specializations

Tending toward Bipedal Life [cf. Fig. 38, p. 62]) Order Thecodontia. Triassic ancestors of dinosaurs, birds, and others.

Order Crocodilia. Crocodiles and alligators; degenerate amphibious survivors of archosaur group. Order Pterosauria. Extinct flying reptiles with membrane wing.

Order Saurischia. "Reptile-like" dinosaurs with triradiate pelvis. Carni-

vores and large amphibious forms. Order Ornithischia. "Birdlike" dinosaurs with tetraradiate pelvis; her-

bivorous. Bipeds (including duckbills), armored and horned quadru-

SUBCLASS SYNAPSIDA (Lateral Temporal Opening; Forms Leading to Mammals, Extinct)

Order Pelycosauria. Primitive Permian mammal-like reptiles, close to stem reptiles.

Order Therapsida. Advanced mammal-like forms of late Permian and Triassic (Fig. 42, p. 68).

#### Class Aves

(Winged Archosaur Descendants, with Feathers, Temperature Control, and so forth)

SUBCLASS ARCHAEORNITHES (Primitive Jurassic Fossil Birds with Many Repullian Characters [Fig. 39, p. 64])

SUBCLASS NEORNITHES (All Other, "Modernized," Birds)

Superorder Odontognathae. Toothed birds of the Cretaceous.

Superorder Palaeognathae. Including mainly the ostrich-like birds, or ratites, with relatively primitive structures (Fig. 40, p. 65).

Superorder Neognathae. All remaining birds, arranged in a considerable number of orders, but all essentially similar in most anatomic features (Fig. 41, p. 66).

# Class Mammalia

(Animals with Hair, Nursing Habit, Brain of Advanced Type, and so on) SUBCLASS PROTOTHERIA (Egg-Laying Mammals)

Order Monotremata. The duckbill and spiny anteater of the Australian region.

SUBCLASS THERIA (Mammals Bearing the Young Alive)

Infraclass and Order Pantotheria. Small Jurassic fossil mammals, probably ancestral to remaining groups. (There are several further Jurassic orders of obscure relationships.)

Infraclass Allotheria, Order Multituberculata. An extinct group of primitive but aberrant mammals, perhaps comparable in habits to later rodents. Jurassic to Eocene.

Infraclass Metatheria, Order Marsupialia. The pouched mammals, as opossum and many Australian types. Young born alive, but at immature stage.

Infraclass Eutheria. The higher mammals, with an efficient placenta (Fig. 44, p. 71).

Order Insectivora. Ancestral placentals and modern descendants, such as shrews, moles, hedgehog.

Order Chiroptera. Bats.
Order Primates. Essentially an arboreal offshoot of the primitive placental stock (Fig. 45, p. 72).

SUBORDER LEMUROIDEA (PROSIMII). Tree shrews and lemurs.

Suborder Tarsioldea. Tarsius and extinct relatives, transitional between lemurs and monkeys.

SUBORDER ANTHROPOIDEA. Monkeys, apes, and man.

Infraorder Platyrrhini. South American monkeys, with nostrils opening sideways.

Family Hapalidae. Marmosets.

Family Cebidae. Typical South American monkeys.

Infraorder Catarrhini. Old World monkeys, apes, and man; nostrils open downward.

Family Cercopithecidae. Old World monkeys.

Family Simiidae. Manlike apes.

Family Hominidae. Men.

Order Carnivora. The carnivores (Fig. 46, p. 74).

SUBORDER CREODONTA. Extinct archaic carnivores.

SUBORDER FISSIPEDIA. Modern land carnivores.

Infraorder Eucreodi. Extinct ancestors of modern types.

Infraorder Arctoidea. Extinct ancestors of modern type

Infraorder Arctoidea. The dogs and relatives.

Family Mustelidae. Primitive. Weasels, skunks, badgers, otters, and so on.

Family Canidae. Dogs, wolves, foxes.

Family Procyonidae. Raccoons, pandas, kinkajous.

Family Ursidae. Bears.

Infraorder Aeluroidea. The "cats" and relatives.
Family Viverridae. Civets, mongoose, and the like; primitive Old
World aeluroids

Family Hyaenidae. Hyenas.

Family Felidae. Cats, lions, tigers, and others.

Suborder Pinnipedia. Marine carnivores: seals, sea lion, walrus.

Order Condylarthra. Primitive extinct ungulates.

Orders Amblypoda, Dinocerata, Embrithopoda, Astrapotheria, Litopterna, Notoungulata. Extinct orders of ungulates, mainly of archaic character, the last three characteristic of South America.

Order Perissodactyla. Odd-toed ungulates (Fig. 47, p. 75).
SUBORDER HIPPOMORPHA.

Family Equidae. Horses, asses, zebras.

Family Titanotheriidae. Titanotheres—large, ungainly, horned, fossil forms.

Family Chalicotheriidae. Extinct forms related to the last twobut with claws, not hoofs.

SUBORDER TAPIROMORPHA.

Family Tapiridae. Tapirs.

Family Rhinocerotidae. Rhinoceroses.

Order Artiodactyla. Even-toed ungulates (Fig. 48, p. 76).

SUBORDER SUINA. Relatively primitive types with simple stomachs, including the following living families as well as several extinct ones:

Family Suidae. Pigs of the Old World.

Family Dicotylidae. Peccaries of the New World.

Family Hippopotamidae. The hippopotamus.

Suborder Ruminantia. Cud chewers, with complex stomach, and selenodont teeth.

Infraorder Tylopoda. Primitive cud chewers, including, in addition to early extinct families:

Family Camelidae. Camels, llamas.

Family Oreodontidae. The oreodons, short-legged ruminants abundant in North American fossil deposits.

Infraorder Pecora. Advanced ruminants, mostly with horns or antlers, including, besides extinct forms:

including, besides extinct forms: Family Tragulidae. Chevrotains, tiny, hornless, deerlike animals

of the tropical Old World. Family Cervidae. The deer tribe.

Family Giraffidae. The giraffe and okapi of Africa.

Family Antilocapridae. The American pronghorn.

Family Bovidae. The cattle family, mainly Old World forms, including bison, sheep, goats, and numerous types of antelopes. Order Hyracoidea. The conies of Africa and Syria; rabbit-like in habits, but actually ungulates. This order and the next two are the subungulate orders—related, and probably of African origin.

Order Proboscidea. The elephants and fossil relatives, mammoths and mastodons.

Order Sirenia. The sea cows—manatee and dugong; an aquatic offshoot of an ungulate stock.

Order Cetacea. Whales.

SUBORDER ARCHAEOCETI. Extinct ancestral whales.

SUBORDER ODONTOCETI. The toothed whales, porpoises, dolphins.

SUBORDER MYSTICETI. Whalebone whales.

Order Edentata. So-called "toothless" mammals, developed in South America.

Suborder Pilosa. Hairy edentates.

Infraorder Gravigrada. Extinct ground sloths.

Infraorder Tardigrada. Family Bradypodidae. Tree sloths.

Infraorder Vermilingua. Family Myrmecophagidae. South American anteaters.

SUBORDER LORICATA. Armored edentates.

Family Dasypodidae. Armadillos.

Family Glyptodontidae. The extinct giant glyptodonts.

Order Tubulidentata. The aardvark of Africa; an anteater, but not related to the preceding order.

Order Pholidota. The Old World pangolin, an anteater, but not closely related to the last two orders.

Order Rodentia. Gnawing animals (except rabbit group). A number of subgroups, of which the most important are:

SUBORDER SCIUROMORPHA. Squirrels, gophers, woodchuck, and others.

SUBORDER CAVIAMORPHA. Guinea pig and many other South American rodents, New World porcupines.

SUBORDER MYOMORPHA. Rats and mice.

Order Lagomorpha. Hares and rabbits; gnawing forms, but not closely related to last order.

2

# SCIENTIFIC TERMINOLOGY

In anatomic terminology common Latin (or Greek) words are used as such for any part of the body for which the ancients had a name. For numerous other structures, scientific names have been invented (1) by using, in a new sense, some classical word which seemed to be descriptive of the part concerned, or (2) commonly, by combining Greek or Latin roots to form a new compound term. The student frequently attempts to memorize such terms without understanding their meaning and with consequent mental indigestion. We give here the roots from which many of these descriptive terms and compounds are derived, as an aid to comprehension. As will be seen, some names formed by the anatomists are rather fanciful or far-fetched; some are none too appropriate. This list is not intended, of course, as a glossary or dictionary of scientific words. We have not, for instance, included common names of bones and muscles. Most of the terms used in this book are defined or discussed in the text. For a wider vocabulary, use of a standard biologic or medical dictionary\* is recommended, but the larger editions of Webster and the like are satisfactory in most regards. Abbreviations: F., French; G., Greek; L., Latin; NL., "New" Latin; Sp., Spanish.

Abdomen. L., from åbdere (β, 10 hide Abdueens. L., ab, away, + ducens, leading. Abduetor. L., ab, away, + ducere, to lead. Accessory. L., accessorius, supplementary. Acelous. C., a, not, + koiles, hollow. Acetabulum. L., acetabulum, vinegar cup. Acoustic. G., adoustikos, pertaining to hearing. Acrania. G., a, without, + krania, heads. Acrdont. G., akron, height or extremity. + odous, tooth,

A-, ab. L. prefix implying separation.

Acromion. G., akron, height or extremity, + omos, shoulder.
\*Such as Dorland, W. A. N.: American Illustrated Medical Dictionary, 23rd ed. Philadelphia V

<sup>\*</sup> Such as Dorland, W. A. N.: American Illustrated Medical Dictionary. 23rd ed. Philadelphia, W. B. Saunders Company, 1957.

Ad. L. prefix, to, toward, at, or near.

Adductor. L., ad, to, + ducere, to lead.

Adrenal. L., ad, near, + renes, kidneys.

Allsphenoid. L., ala, wing, + G., sphen, wedge, + G., eidos, form.

Allantois. G., allas, sausage, + eidos, form, appearance. Alveolus. L., alveolus, little cavity.

Ambiguus. L., ambiguus, uncertain, changeable.

Amnion. G., amnion, fetal membrane.

Amphi-. G. prefix, on both sides; hence, around or double.

Amphibia. G., amphi, double, + bios, life.

Amphicelous. G., amphi, both, + koilos, hollow.

Amphioxus. G., amphi, both, + oxys, sharp.

Amphiplatyan. G., amphi, both, + platys, flat.

Amphistylie. G., amphi, both, + stylos, pillar.

Ampulla. L., ampulla, a flask or vessel swelling in the middle.

A-, an-. G. prefix (alpha privative), without or not.

Ana. G. prefix, on, upward, throughout, frequently, or reinforcing a meaning.

Analogy. G., ana, according to, + logos, due ratio; hence, proportionate. Anamniota. G., an, without, + amnion, fetal membrane.

Anapsid. G., an, not, + apsis, arch.

Anastomosis. G., anastomoein, to bring to a mouth, cause to communicate,

Ankylosis. G., ankylosis, stiffening of the joint.

Annulus. L., anulus (annulus), a ring. Anura. G., an, without, + oura, tail.

Anus. L., anus, fundament.

Apo. G. prefix, from.

Apoda. G., a, without, + poda, feet. Aponeurosis. G., apo, from, + neuron, tendon.

Apophysis. G., apo, from, + physis, growth.

Appendicular. L., appendere, to hang upon.

Arachnoid. G., arachnes, spider, + eidos, shape or likeness.

Arch-, archi-. G. prefix, first or chief; hence, primitive or ancestral.

Archenteron. G., arch, first, + enteron, intestine, gut.

Archipallium. G., archi, first, + pallium, cloak.

Archipterygium. G., archesthai, to begin, + pterygion, a little wing.

Arcualia (pl.). L., arcualis, bow-shaped.

Arrector. L., arrigere, to raise.

Arytenoid. G., arytaina, jug, + eidos, shape or likeness.

Astragalus. G., astragalos, ankle bone, used as a die (commonly pl.).

Atrium. L., atrium, court, entrance hall. Auditory. L., audire, to hear.

Auricle. L. dim., auricula, external ear.

Auto-, G. prefix, autos, self.

Autonomic. G., autos, self, + nomos, law. Autostylie. G., autos, self, + stylos, pillar.

Axial. L., axis, axle of a wheel, the line about which any body turns. Azygos. G., a, not, + zygon, voke; hence, unpaired.

Basal. L., basis, footing or base.

Basi- L. prefix, pertaining to the base.

Basibranchial. L., basis, base, + branchiae, gills.

Basihvoid. L., basis, base, + G., hyoeides, Y-shaped.

Bi- L. prefix, two, twice, or double.

Biceps. L., bis, twice, + caput, head. Bilateral. L., bi, two, + latus, side.

Blasto-, G. prefix, bud, germ, or sprout.

Blastocele. G., blastos, germ, + koilos, hollow.

Blastoderm. G., blastos, germ, + derma, skin.

Blastodisc. G., blastos, germ, + diskos, a round plate, quoit.

Blastomere. G., blastos, germ, + meros, part.

Blastopore. G., blastos, germ, + poros, passage, opening.

Blastula. L. dim. of G. blastos, germ.

Brachial. L., brachialis, belonging to the arm.

Brachium (pl. -ia). L., brachium, arm, especially the forearm.

Branchial. L., branchiae, or G., branchia, gills.

Branchiostegal. G., branchia, gills, + stegein, to cover.

Bronchus. G., bronchia, end of windpipe.

Buccal. L., bucca, cheek.

Bulbus. L., bulbus, bulb, swollen root.

Bunodont. G., bounos, mound, + odous, tooth.

Calcaneum. L., calcaneum, heel.

Callosum. L., callosus, -a, -um, thick-skinned.

Calvx (pl. calices). L., calyx, husk, cup-shaped protective covering.

Caninus. L., caninus, pertaining to a dog.

Capillary. L., capillaris, pertaining to the hair.

Capitulum. L. dim. (caput), small head.

Caput (pl. capita). L., caput, head.

Carapace. NL., carapax, bony or chitinous covering.

Cardiac. G., kardiakos (kardia), pertaining to the heart.

Cardinal. L., cardinalis, pertaining to a door hinge. Carnassial. F., carnassier, carnivorous (L., caro, carnis, flesh).

Carnivorus. L., caro, flesh, + vorare, to devour.

Carnosus. L., carnosus, fleshy. Carpus. G., karpos, wrist.

Cartilago (pl. -agines). L., cartilago, gristle, cartilage.

Caudal. L., cauda, tail.

Cava. L., cavus, -a, -um, hollow.

Cavernosus. L., caverna, a hollow or cave.

Cecum. L., caecus, -a, -um, blind.

Celiac. G., koilia, belly.

Celom (e). G., koiloma, a hollow. Cephalic. G., kephale, head.

Cephalo-. G. combining form, kephale, head.

Ceratobranchial. G., keras, horn, + branchia, gills.

Ceratotrichia. G., keras, horn, + thrix, hair.

Cerebellum. L. dim., cerebrum, brain.

Cerebrum. L., cerebrum, brain.

Cervical. L., cervix, neck.

Chiasma, G., chiasma, figure of X.

Choana (pl. -ae). G., choane, funnel.

Choledochus. G., chole, bile, + dochos (dechomai), container.

Chondrichthyes. G., chondros, cartilage, + ichthys, fish.

Chondro-. G., combining form, cartilaginous.

Chondroblast. G., chondros, cartilage, gristle, + blastos, shoot or germ.

Chondroclast. G., chondros, cartilage, + klaein, to break.

Chorda. G., chorde, string of gut, cord. Choroid. G., chorion, skin, + eidos, likeness.

Chorion. G., chorion, skin.

Chromaffin. G., chroma, color, + L., affinis, showing affinity for.

Chromatophore. G., chroma, color, + pherein, to bear. Chromosome. G., chroma, color, + soma, body.

Chyme. G. chymos, juice.

Ciliary. L., cilium (pl. cilia), eyelash.

Circum-. L. prefix, around. Cloaca. L., cloaca, sewer, drain.

Cnemial. G., kneme, lower leg.

Cochlea. L., cochlea (G., kochlias), spiral, snail shell.

Colon. L., colon, great gut. Columella. L. dim. (columna), little pillar.

Commissure. L., commissura (cum + mittere), connection.

Concha. L., concha, bivalve, oyster shell.

Condyle. G., kondylos, knuckle. Conjunctiva. L., conjunctivus, connecting.

Constrictor. L., constringere, to draw together.

Coprodeum. G., kopros, dung, + hodaios, pertaining to a way.

Corium. G., chorion, skin, leather.

Cornea. L., corneus, horny.

Coronary. L., coronarius, pertaining to a wreath or crown; hence, encircling. Cortex. L., cortex, bark, rind.

Cortical. L., cortex, icis, bark, rind.

Cosmin. G., kosmos, orderly arrangement, + eidos, form.

Costa. L., costa, rib. Costal. L., costa, rib.

Cranial. G., kranion, skull.

Cribriform. L., cribrum, sieve, + forma, form.

Cricoid. G., krikos, ring, + eidos, form.

Crista. L., crista, crest. Crus (pl. crura). L., crus, leg.

Ctenoid. G., kteis (gen. ktenos), a comb, + eidos, form.

Cuneiform. L., cuneus, wedge, + forma, shape. Cutis. L., cutis, skin.

Cvcloid. G., kyklos, circle, + eidos, form. Cystic. G., kystis, the bladder, a bag or pouch.

Cytoplasm. G., kytos, cell, + plasma, plasma, anything molded.

De . L. prefix signifying down, away from, deprived of. Deciduous. L., deciduus (de + cado), falling off.

Decussatio. L., decussatio, crosswise intersection.

Decussation. L., decussatio, intersection of two lines, as in Roman X.

Deferens. L., de, away, + ferens, carrying.

Dens. L., dens, dentis, tooth.

Depressor. L., de, down, + premere, to press.

Dermal, G., derma, skin.

Dermatome. G., derma, skin, + temnein, to cut. Di-, dia-. G. prefix, through, between, apart, across.

Di-. G., dis, twice; hence, twofold or double.

Diaphragm. G., diaphragma, partition, midriff. Diaphysis. G., dia, between, + physis, growth.

Diapophysis. G., dia, apart, + apophysis, outgrowth. Diapsid. G., di, double, + apsis, arch.

Diarthrosis. G., dia, through, + arthroun, to fasten by a joint.

Diastema (pl. -ata). G., diastema, interval.

Digit. L., digitus, finger.

Diphycercal. G., diphyes, twofold, + kerkos, tail.

Diplospondylous. G., diploos, double, + spondyle, vertebra.

Dipnoi. G., di, double, + pnein, to breathe.

Distal. L., distare, to stand apart.

Dorsal. L., dorsum, back.

Duct. L., ducere, to lead or draw.

Duodenum. L., duodeni, twelve (meaning twelve fingerbreadths).

E-, ex-. L. prefix, out, out of, from.

Ectepicondyle. G., ek, out, + epi, upon, + kondylos, knuckle, knob.

Ectoderm. G., ektos, outside, + derma, skin.

Effector. L., efficere, to bring to pass.

Efferent. L., ex, out, + ferre, to bear.

Eiaculatory. L., e, out, + jacere, to throw.

Ek-, ekto-. G. prefix, out of, from, outside.

Embolomerous. G., en, in + ballein, to throw, + meros, portion or part.

En-, endo-. G. prefix, in, within.

Endocardium. G., endon, within, + kardia, heart.

Endochondral, G., endon, within, + chondros, cartilage.

Endocrine. G., endon, within, + krinein, to separate.

Endoderm. G., endon, within, + derma, skin.

Endolymph. G., endon, within, + L., lympha, water.

Endometrium. G., endon, within, + metra, womb.

Endoneurium. G., endon, within, + neuron, nerve.

Endoskeleton. G., endon, within, + skeletos, dried up.

Endostyle. G., endon, within, + stylos, pillar.

Endothelium. G., endon, within, + thele, nipple. Entepicondyle. G., entos, in, + epi, upon, + kondylos, knuckle.

Enzyme. G., en, in, + zyme, leaven.

Ependyma. G., ependyma, upper garment.

Epiaxial. G., epi, on, + axis, center line.

Epibranchial. G., epi, on, + branchia, gills.

Epicardium. G., epi, on, + kardia, heart.

Epicondyle. G., epi, on, + kondylos, knuckle.

Epidermis. G., epi, on, + derma, skin. Epididymis. G., epi, on, + didymoi, testicles.

Epiglottis. G., epi, on, + glotta, tongue.

Epimere. G., epi, on, + meros, part.

Epineurium. G., epi, on, + neuron, nerve.

Epiphysis. G., epi, on, + physis, growth.

Epiploic. G., epiploon, caul, omentum.

Epithalamus. G., epi, on, + thalamos, chamber.

Epithelium. G., epi, on, + thele, nipple. Erythrocyte. G., erythros, red, + kytos, cell,

Esophagus. G., oisein (phero), to carry, + phagein, to eat.

Ethmoid. G., ethmos, sieve, + eidos, form.

Excretion. L., (excretus) ex, out, + cernere, to sift.

Exocrine. G., ex, out, + krinein, to separate.

Extensor. L., ex, out, + tendere, to stretch. Extrinsic. L., extrinsecus, on the outside.

Facialis. L., facies, face.

Falciform. L., falx, sickle, + forma, shape.

Falx. L., falx, falcis, sickle.

Fascia (pl. -iae). L., fascia, band.

Fiber. L., fibra, string, thread.
Fibril. NL., fibrilla, a little thread.

Filoplume. L., filum, thread, + pluma, soft leather, down.

Filum. L., filum, thread.

Fimbria. L., fimbriae, threads, fringe.

Firmisternal. L., firmus, steadfast, strong, + G., stemon, chest.

Fissure. L., fissura (findo), a cleft.

Flagellum (pl. -a). L., flagellum, a little whip.

Flexor. L., flexus, bent. Flocculus. NL. dim. (floccus), a tuft of wool.

Follicle. L., folliculus, a small bag. Fornix. L., fornix, arch or vault.

Fovea. L., fovea, small pit.

Frontal. L., frons, frontis, forehead, brow.

Fundus. L., fundus, bottom. Funiculus. L., funiculus, a slender rope.

Gametes. G., gametes, spouse.

Ganglion. G., ganglion, a swelling under the skin.

Gastralia (pl.). G., gaster, belly

Gastrula. NL. dim. (from G., gaster, stomach).

Geniculate. L., geniculatus, with bent knee. Genital. L., genitalis (gigno), pertaining to birth.

Germinal. L., germen, bud, germ.

Germinative. L., germen, bud, germ.

Glans. L., glans, acorn.

Glenoid. G., glene, socket, + eidos, form.

Glomerulus. L. dim. of glomus, a ball. Glomus (pl. glomera). L., glomus, ball.

Glossopharyngeus. G., glossa, tongue, + pharynx, throat.

Glottis. G., glottis, mouth of the windpipe,

Gluteus. G., gloutos, rump. Gnathos. G., gnathos, jaw.

Gnathostomata (pl.). G., gnathos, jaw, + stoma, mouth.

Gonad. G., gone, seed.

Granulocytes. L., granulum, small grain, + G., kytos, cell.

Granulosus. L., granulosus, full of grains.

Granulum. L., granulum, small grain.

Guanin (e). Sp., guano, dung of sea fowl.

Guanophore. Sp. from Peruvian, huanu, dung, + G., pherein, to bear.

Gubernaculum. L., gubernaculum, helm.

Gular. L., gula, throat.

Gyrus (pl. gyri). G., gyros, a turn. Habenula. L., habena, strap.

Haemal, hemal, G., haima, blood,

Hamatum. L., hamatus, hook-shaped.

Hemi. G. prefix, signifying half.

Hemibranch. G., hemi, half, + branchia, gills. Hemichordata. G., hemi, half, + chorde, string.

Hemipenis. G., hemi, half, + L., penis, penis.

Hemisphere, G., hemi, half, + sphaira, hall. Hemocytoblast. G., haima, blood, + kytos, cell, + blastos, germ.

Hemoglobin. G., haima, blood, + L., globus, sphere.

Hemopoietic. G., haima, blood, + poietikos, creative.

Hepatic. L., hepar, liver.

Hetero. G. combining form signifying other, different.

Heterocelous. G., heteros, other, + koilos, hollow.

Heterocercal, G., heteros, other, + kerkos, tail.

Heterodont. G., heteros, other, + odous, tooth.

Heterotopic. G., heteros, other, + topos, place.

Hippocampus. G., hippos, horse, + kampos, sea monster.

Histology, G., histos, web, + logos, discourse, account.

Holo-. G. combining form signifying whole.

Holoblastic. G., holos, whole, + blastos, germ.

Holobranch. G., holos, whole, + branchia, gills.

Holocephali. G., holos, whole, + kephale, head.

Holonephros. G., holos, whole, + nephros, kidney. Holostei, G., holos, whole, + osteon, bone,

Homo-. G. combining form signifying one and the same.

Homocercal. G., homos, same, + kerkos, tail.

Homoiothermous. G., homos, same, + thermos, hot.

Homolecithal. G., homos, same, + lekithos, yolk.

Homology. G., homos, same, + logos, ratio.

Hormone, G., hormaein, to excite,

Humor. L., humor, moisture, fluid.

Hyaline. G., hyalos, glass.

Hvoid. G., hvoeides, U-shaped.

Hyomandibular. G., upsilon (Y-shaped letter) + L., mandibula, jaw. Hyostylie. G., upsilon (Y-shaped letter) + stylos, pillar.

Hypaxial. G., hypo, under, + L., axis, center line, axis.

Hypo-. G. prefix signifying under, below.

Hypobranchial. G., hypo, below, + branchia, gills.

Hypoglossal. G., hypo, under, + glossa, tongue. Hypomere. G., hypo, under, + meros, part.

Hypophysis. G., hypo, under, + physis, growth.

Hypothalamus. G., hypo, under, + thalamos, chamber, couch.

Hypsodont. G., hypsos, height, + odous, tooth.

Hypural. G., hypo, under, + oura, tail. Heum. G., eilein, to wind or turn.

In-. L. prefix signifying not; also signifying in, into, within, toward, on. Incisor. L., incisus (incidere), cut.

Incus. L., incus, anvil.

Inductor. L., inducere, to lead on, excite.

Infra-. L. prefix signifying below, lower than.

Inframeningeal. L., infra, below, + G., meninx, membrane.

Infraparietal. L., infra, below, + paries, wall.

Infraspinous. L., infra, below, + spina, spine. Infundibulum. L., infundibulum, a funnel.

Inguinal. L., inguina, groin.

Integument. L., in, over, + tegere, to cover.

Inter-. L. prefix signifying between, among.

Intercalated. L., inter, between, + calare, to call.

Intercostal. L., inter, between, + costa, rib.

Intermaxillary. L., inter, between, + maxilla, jaw.

Interrenal. L., inter, between, + renes, kidneys.

Interstitial. L., inter, between, + sistere, to set.

Intervertebral. L., inter, between, + vertebra, joint. Intestine. L., intus, within.

Intrinsic. L., intrinsecus, inward.

Invagination. L., in, in, + vagina, sheath. Invertebrate. L., in, not, + vertebratus, jointed.

Iridocyte. G., iris, idos, rainbow, + kytos, cell.

Iris. G., iris, rainbow.

Ischiofemoral. G., ischion, hip, + L., femur, thigh.

Ischium (pl. -ia). G., ischion, hip. Iso-. G. prefix signifying equal.

Isolecithal. G., isos, equal, + lekithos, volk.

Isomer. G., isos, equal, + meros, part. Jejunum. L., jejunus, empty (of food).

Jugal. L., jugum, voke.

Jugular. L., jugularis (jugulum), pertaining to the neck.

Labial. L., labialis (labia), pertaining to the lips.

Lacerate. L., lacerare, to tear. Lacrimal. L., lacrima, tear.

Lagena. L., lagena, flask.

Lamina (pl. -ae). L., lamina, thin plate.

Larva (pl. -ae). L., larva, ghost, mask.

Larynx. G., larynx, upper part of windpipe. Lateral. L., lateralis (latus), pertaining to a side.

Lepidotrichia. G., lepis, scale, + thrix, hair.

Leukocyte. G., leukos, white, + kytos, cell,

Levator. L., levare, to raise.

Ligamentum. L., ligamentum, a bandage. Lipid. G., lipos, fat, + eidos, resemblance.

Lipo-. G. combining form signifying fat.

Lipophore. G., lipos, fat, + phoros (phero), bearing. Lobus. G., lobos, lobe.

Lophodont. G., lophos, ridge, + odous, tooth.

Lucidum. L., lucidus (lux), full of light, clear.

Lumbar. L., lumbare, apron for the loins.

Luteum. L., luteus, yellow.

Lymphoevte. L., lympha, water, + G., kytos, cell.

Macrophage. G., makros, large, + phagein, to eat.

Macula. L., macula, spot, stain.

Malleus. L., malleus, hammer.

Mammillary. L., mamillaris (mamma, -ae), of or in the breast.

Marginal. L., marginalis (margo), bordering.

Marsupium. L., marsupium, pouch.

Mastoid. G., mastos, breast, + eidos, resemblance.

Matrix. L., matrix (mater), womb, groundwork, or mold.

Meatus (pl. -us). L., meatus, passage.

Medial. L., medialis (medius), pertaining to the middle.

Mediatinum. L., mediatis (medius), pertaining to the Mediastinum. L., mediastinus, servant, drudge.

Medulla. L., medulla, marrow, pith.

Melanin. G., melas, melanos, black.

Membrane. L., membrana, skin.

Meninx (pl. meninges). G., meninx, membrane.

Mes-, meso-. G. prefix signifying middle.

Mesencephalon. G., mesos, middle, + en, in, + kephale, head. Mesenchyme. G., mesos, middle, + en, in, + chymos, juice.

Mesentery. G., mesos, middle, + en, in, + chymos, ju Mesentery. G., mesos, midway between, + enteron, gut.

Mesocardium, G., mesos, middle, + kardia, heart.

Mesoderm. G., mesos, middle, + derma, skin.

Mesolecithal. G., mesos, middle, + lekithos, yolk.

Mesonephros. G., mesos, middle, + nephros, kidney.

Mesoptervgium. G., mesos, middle, + ptervgion, little wing.

Mesorchium. G., mesos, middle, + prerygion, Mesorchium. G., mesos, middle, + orchis, testis.

Mesovarium. G., mesos, middle, + L., ovarium, ovary.

Meta-. G., prefix meaning after, next; denoting change of time or situation.

Metabolic. G., metabole, change.

Metacarpus. G., meta, after, + L., carpus, wrist.

Metacarpus. G., meta, after, + L., carpus, wrist.
Metamere. G., meta, after, + meros, part.

Metamorphosis. G., meta, signifying change, + morphe, form.

Metanephros. G., meta, after, + nephros, kidney.

Metapleura. G., meta, after, + pleura, side.

Metapodial. G., meta, after, + pous, podos, foot. Metatarsus. G., meta, after, + L., tarsus, ankle.

Metencephalon. G., meta, after, + enkephalos, brain.

Molar. L., molaris (mola), pertaining to a millstone.

Monocyte. G., monos, single, + kytos, cell.

Mucus. L., mucus, snivel, slippery secretion.

Multangulum. L., multus, many, + angulus, angle.

Myelencephalon. G., myelos, marrow, + enkephalos, brain.

Myelin. G., myelos, marrow.

Myo-. G. combining form signifying muscle.

Myocardium. G., mys, myos, muscle, + kardia, heart.

Myocomma. G., mys, myos, muscle, + komma, implying separation.

Myodome. G., mys, myos, muscle, + L., domus, house. Myomere. G., mys, myos, muscle, + meros, part.

Neopallium. G., neos, youthful, new, + L., pallium, cloak.

Myotome. G., mys, myos, muscle, + tome, a cutting. Naris (pl. -es). L., naris, nostril.

Nephridia. G., nephridios, belonging to the kidneys.

Nephrotome. G., nephros, kidney, + tome, a cutting. Neural. G., neuron, nerve.

Neurenterie. G., neuron, nerve, + enteron, gut.

Neurilemma. G., neuron, nerve, + lemma, husk, sheath.

Neuro-. G. combining form signifying nerve. Neuroglia. G., neuron, nerve, + gloia, glue.

Neurohumor. G., neuron, nerve, + L., humor, fluid.

Neuromast. G., neuron, nerve, + mastos, round hill.

Neuron. G., neuron, sinew, tendon; equivalent of L. nervus; whence, nerve.

Neuropil. G., neuron, nerve, + pilos, felt.

Nictitating. L., nictare, to wink.

Nidamental. L., nidamentum, materials for a nest.

Node. L., nodus, knot.

Notochord. G., noton, back, + chorde, cord.

Nuchal. L., nucha, nape of the neck.

Obliquus, L., obliquus, slanting.

Oculomotor. L., oculus, eye, + motor, mover.

Odontoblast. G., odous, tooth, + blastos, shoot, germ. Olecranon. G., olekranon, point of the elbow.

Olfactory. L., olere, to smell, + facere, to make.

Omasum. L., omasum, paunch.

Omentum. L., omentum, adipose membrane enclosing the bowels.

Omphalo-. G. combining form (omphalos) signifying the navel. Ontogeny. G., onta, things that exist, + gennan, to beget.

Operculum. L., operculum, lid.

Ophthalmic. G., ophthalmos, eye.

Opistho. G. prefix signifying backward, behind.

Opisthocelous. G., opisthe, behind, + koilos, hollow.

Opisthonephros. G., opisthe, behind, + nephros, kidney. Optic. G., opsis, sight.

Osseous. L., os (pl. ossa), bone.

Ossiele. L., ossiculum, small bone. Osteoblast. G., osteon, bone, + blastos, germ.

Osteocyte. G., osteon, bone, + kytos, cell.

Otic. G., otikos, belonging to the ear. Otolith. G., ous, otos, ear, + lithos, stone.

Ovum (pl. ova). L., ovum, egg.

Oxyphil. G., oxys, acid, + philos, friend.

Paleontology. G., palaios, ancient, + onta, existing things, + logos, science.

Paleopallium. G., palaios, ancient, + L., pallium, covering. Pallium. L., pallium, cloak.

Palma. L., palma, the (open) hand.

Palpebra. L., palpebra, eyelid.

Pancreas. G., pan, all, + kreas, flesh.

Papilla. L., papilla, pimple.

Para-. G. prefix signifying alongside of, near.

Parabronchii. G., para, beside, + bronchos, windpipe.

Paracentrum. G., para, near, + kentron (L. centrum), center.

Parachordal. G., para, beside, + chorde, cord.
Paraganglion. G., para, along, beside, + ganglion, knot.

Paraphysis. G., para, beside, + physis, growth.

Parapsid. G., para, beside, + apsis, arch.

Parathyroid. G., para, near, + thyreos, oblong shield, + eidos, form.

Parencephalon. G., para, beside, + enkephalon, brain.

Parietal. L., paries, wall.

Parotid. G., para, near + ous, otos, ear.

Pecten. L., pecten, comb.

Pectoral. L., pectoralis (pectus), belonging to the breast.

Pedunculus. L., pediculus, a little foot.

Pelvic. L., pelvis, basin.

Peri-. G. prefix meaning around.

Pericardial. G., peri, around, + kardia, heart.

Perichondrium. G., peri, around, + chondros, cartilage.

Perichordal. G., peri, around, + chorde, cord.

Perilymph. G., peri, around, + L., lympha, fluid.

Perimysium. G., peri, around, + mys, muscle.

Periosteum. G., peri, around, + osteon, bone.
Peristalsis. G., peristaltikos, clasping and compressing.

Peritoneum. G., peritonaion, membrane containing the lower viscera.

Phallie. G., phallikos, pertaining to the penis.

Pharynx. G., pharynx, throat.

Photophore. G., phos, photos, light, + pherein, to bear.

Phylogeny. G., phylon, race, + gennan, to beget.

Pineal. L., pinea, pine cone. Pinna (pl. -ae). L., penna, pinna, feather; hence, wing.

Pisiform. L., pisum, pea, + forma, shape.

Pituitary. L., pituita, slime, phlegm.

Placenta. L., placenta, a flat cake. Placode. G., plax, plate, + eidos, likeness.

Placode. G., plax, plate, + eidos, Planta. L., planta, sole of the foot.

Plastron. F., plastron, breastplate.

Platybasie. G., platys, broad, flat, + L., basis, base.

Plectrum. G., plektron, hammer.

Pleuro-. G. combining form signifying the side.

Pleurocentrum. G., pleura, side, + kentron (L., centrum), center.

Pleurodont. G., pleura, ribs, side, + odous, tooth. Plexus (pl. -us). L., plexus, plaiting, braid.

Pneumatic. G., pneumatikos, pertaining to breath.

Poikilothermous. G., poikilos, changeful, + thermos, heat.

Pons. L., pons, pontis, bridge.

Portal. L., porta (pl. -ae), gate.

Porus. G., poros, passage.

Prae-, pre-. L. prefix signifying before, in front.

Premolar. L., pre, in front, + molaris, molar.

Prepuce. L., praeputium, foreskin.

Primordial. L., primordium, beginning.

Pro-. G. or L. prefix signifying before, in front of, or prior.

Procelous. G., pro, in front, + koilos, hollow.

Proctodeum. G., proktos, anus, + hodaios, pertaining to a way. Profundus. L., profundus, deep.

Pronator. L., pronare, to bend forward.

Pronephros. G., pro, before, + nephros, kidney.

Proprioceptor. L., proprius, special, + capere, to take. Prosencephalon. G., pros, before, + enkephalos, brain.

Prostate. L., pro, in front, + stare, to stand.

Protonephros. G., protos, first, + nephros, kidney.

Protoplasm. G., protos, first, + plasma, form. Proximal. L., proximus, next.

Pseudobranch. G., pseudes, false, + branchia, gills.

Pterygoid. G., pteryx, wing, + eidos, likeness.

Pterylae. G., pteron, feather, + hyle, a wood. Pubis (pl. -es). L., pubis, mature.

Pulmonary. L., pulmo, lung.

Pygal. G., pyge, rump.

Pygostyle. G., pyge, rump, + stylos, pillar.

Pylorus. G., pylouros, gate-keeper.

Pyriform. L., pirum, pear, + forma, shape. Quadriceps. L., quattuor, four, + caput, head.

Quadrigeminus. L., quadrigeminus, fourfold, four.

Radial. L., radius, rod, spoke. Receptor. L., recipere, to take back, receive,

Rectus. L., rectus, straight.

Remiges (pl.). L., remex, rower.

Renal. L., renes, kidneys. Rete. L., rete, network.

Reticulum. L., reticulum, a little net.

Retina. L., rete, net.

Retractor. L., retrahere, to draw back.

Retrices. L., retro, back, + cedere, to go.

Rhachitomous. G., rhachis, spine + temnein, to cut. Rhinal. G., rhis, nose.

Rhombencephalon. G., rhombas, kind of parallelogram, + enkephalos, brain.

Rostrum (pl. -a). L., rostrum, beak. Rotator. L., rotare, to whirl about.

Ruminare. L., ruminari, to chew the cud.

Sacculus. L., sacculus, a little bag. Sacrum. L., sacer, sacred.

Sagittal. L., sagitta, arrow. Salpinx. G., salpinx, trumpet.

Sarcolemma. G., sarx, flesh, + lemma, husk, skin.

Scala. L., scala, staircase. Sclera. G., skleros, hard.

Sclerotic. G., skleros, hard.

Sclerotome. G., skleros, hard, + temnein, to cut.

Scrotum. L., scrotum (scrotum), skin.

Sebaceous. L., sebum, tallow, grease.

Selenodont. G., selene, moon (hence, crescent), + odous, tooth.

Seminiferous. L., semen, seed, + ferre, to bear.

Septum. L., saeptum, fence.

Sinus (pl. -us). L., sinus, curve, cavity, bosom.

Somatic. G., soma (pl. somata), body.

Somatopleure. G., soma, body, + pleura, side.

Somite. G., soma, body, + suffix -ite, indicating origin.

Spermatozoon (pl. -a). G., sperma, seed, + zoon, animal.

Sphenoid. G., sphen, wedge, + eidos, likeness.

Sphineter. G., sphingein, to bind tight.

Spina. L., spina, thorn.

Spiracle. L., spiraculum, air hole.

Splanchnic. G., splanchna, viscera.

Splanchnopleure. G., splanchna, viscera, + pleura, side.

Stapes. L., stapes, stirrup.

Stereospondylous. G., stereos, solid, + sphondylos, vertebra.

Stomodeum. G., stoma, mouth, + hodaios, pertaining to a way.

Stratus (pl. strata). L., stratus, layer.

Striatum. L., striatus, grooved, streaked.

Styloid. G., stylos, pillar, + eidos, likeness.

Sub-. L. prefix signifying under, beneath, near.

Subcostal. L., sub, under, + costa, rib.

Sublingual. L., sub, under, + lingus, tongue.

Subunguis. L., sub, under, + unguis, nail.

Subvertebral. L., sub, under, + vertebra, joint.

Suleus, L., suleus, furrow.

Supinator. L., supinare, to bend backward. Supracostal. L., supra, above, + costa, rib.

Supraspinatus. L., supra, above, + spina, thorn.

Sym-, syn-. G. prefix signifying with or together.

Sympathetic. G., syn, together, + pathein, to suffer.

Symphysis. G., syn, together, + physis, growth.

Synapse. G., syn, together, + haptein, to fasten.

Synarthrosis. G., syn. together, + arthron, joint.

Synsaerum. G., syn, together, + L., sacer (os sacrum), sacrum.

Syrinx. G., syrinx, pipe.

Tabular. L., tabula, board, table.

Talonid. L., talus, heel, + G., eidos, form.

Tapetum. L., tapete, carpet.

Tarsus. G., tarsos, sole of the foot.

Tectum. L., tectum (tego), roof.

Tegmentum. L., tegumentum, a covering.

Tela. L., tela, web.

Telencephalon. G., telos, end, + enkephalos, brain. Telolecithal. G., telos, end, + lekithos, yolk.

Temporal. I., temporalis, belonging to time.

Temporal. L., tempora, the temples.

Tendon. L., tendere, to stretch.

Tentorium. L., tentorium, tent.

Terminalis. L., terminare, to limit.

Testis. L., testis, testicle.

Tetrapod. G., tetra, four, + pous, foot.

Thalamus. G., thalamos, chamber or couch.

Thecodont. G., theke, case, sheath, + odous, tooth.

Thorax (thoracis). G., thorax, breastplate, breast. Thromboeytes. G., thrombos, clot, + kytos, cells.

Thymus. G., thymos, sweethread.

Thyroid. G., thyreos, shield, + eidos, form.

Trabecula (pl. -ae). L., trabecula, a little beam.

Trachea. G., tracheia, windpipe.

Triceps. L., tres, three, + caput, head.

Trigeminus. L., trigeminus, born three together.

Triquetrum. L., triquetrus, three-cornered, triangular.

Trochanter. G., trochos, wheel, pulley.

Trochlea. G., trochilia, pulley.

Trophoblast. G., trophe, nourishment, + blastos, shoot, germ. Tropibasic. G., trope, a turning, + L., basis, base.

Tuberculum. L., tuberculum, a small hump.

Tunica. L., tunica, undergarment.

Turbinal. L., turbo, a top, anything that spins or shows turning.

Tympanie. L., tympanum, drum.

Umbilical, L., umbilicus, navel.

Unciform. L., uncus, hook, + forma, shape.

Uncinate. L., uncinatus, furnished with a hook.

Urea. G., ouron, urine. Urodela. G., oura, tail, + delos, evident.

Urodeum. G., ouron, urine, + hodaios, pertaining to a way.

Urogenital. G., ouron, urine, + L., genitalis, genital.

Uropygial. G., orros, end of os sacrum, + pyge, rump. Urostyle. G., oura, tail, + stylos, pillar.

Uterus. L., uterus, womb.

Utriculus. L., utriculus, small skin or leather bottle.

Vagus. L., vagus, wandering.

Valvula. L., valvula, a little fold or valve.

Vas. L., vas, vessel.

Vascular. L., vasculum, small vessel. Ventral. L., venter, belly.

Ventriele. L., ventriculus, little cavity, loculus. Vermiform. L., vermis, worm, + forma, shape.

Vesicle. L., vesicula, a small bladder.

Vestibulum. L., vestibulum, entrance court.

Vibrissa (pl. -ae). L., vibrissa, hair in the nostril. Villus (pl. villi). L., villus, shaggy hair.

Visceral. L., viscera, entrails, bowels.

Vitelline. L., vitellus, volk of egg.

Vitreus. L., vitreus, of glass; hence, transparent.

Viviparous. L., vivus, living, + parere, to beget. Vomer. L., vomer, ploughshare.

Xiphiplastron. G., xiphos, sword, + F., plastron, breastplate.

Zygapophysis. G., zygon, yoke, + apophysis, process of a bone.

Zygomatic. G., zygoma, cheekbone.

# Latin Word Endings

Although scientific terms are often used in English form, some knowledge of the use of these words in Latin form is desirable. Latin is a highly inflected language, with a variable series of terminations for nouns and adjectives expressing not only singular and plural numbers, but also genders (of an artificial nature) and a variety of cases; still further, there are several different systems of forming such terminations ("declensions"). Fortunately, however, nearly all use of scientific terms involves only two cases—nominative and genitive. Less than a score of endines affixed to the word root will cover most instances.

Adjectives (which must agree in gender, number, and case with their nouns) are "declined" according to one of the two following schemes, for each of which a common adjective is used as an example (the ending, attached to the root, is in holdface).

# First and Second Declension (Combined)

	Masculine	Neuter	Feminine
Nominative singular	magnus	magnum	magna
Nominative plural	magni	magna	magnae
Genitive singular	magni		magnae
Genitive plural	magnorum		magnarum

Th	nird Declension		
	Masculine and Feminine	Neuter	
Nominative singular Nominative plural	grand <b>is</b> grandes	grande grand <b>ia</b>	
Genitive singular Genitive plural		grand <b>is</b> grand <b>ium</b>	

Most nouns follow one of these same schemes. Thus, fibula is a feminine noun of the first declension and is declined fibula, fibulae, fibulae, fibularum; humerus is a masculine noun of the second declension, declined humerus, humeri, humeri, humerorum; sternum, sterna, sterni, sternorum, a neuter noun of the second declension; cutis, cutes, cutis, cutium (skin), a feminine noun of the third declension.

There are, however, two complications: (1) in the third declension most nouns have a short form for the nominative singular, a longer root for the other case endings. Thus femur (third declension neuter) becomes femora, and so on, in other cases; other typical examples are menina, meninges; foramen, foramina, caputa, capita. (2) A few nouns used anatomically belong to a further declension—a fourth declension. Of masculine words of this gender—plexus and meatus are examples—the plural spelling is the same as the singular, hence the English form is preferable for common use. A common neuter noun of this declension is comu (horn), declined comu, cornua, cornua, cornua, cornual.

# 3

# REFERENCES

Below are listed a few of the more useful general works, or works on special topics or animal types, review articles, and a limited number of original research papers and monographs. To look further into the literature of any special topic, these two publications are most useful:

Zoological Record, 1864-date. London.

Each annual volume lists all papers published during the year concerning each class of vertebrates, and follows this with classified lists of those papers which deal with various topics in anatomy, embryology, and so forth.

Biological Abstracts, 1926-date. Philadelphia.

A voluminous journal which attempts to abstract and index all papers published in any field of biology.

In the sections which follow, the more generally useful works are listed first, followed by works of a more specialized nature or more restricted anatomical interest.

## GENERAL

- Bolk, L., Göppert, E., Kallius, E., and Lubosch, W.: Handhuch der vegleichenden Anatomie der Wirbeltiere. 6 vols. Berlin and Vienna, Urban and Schwartzenberg, 1931–1939. A comprehensive work on vertebrate anatomy by many specialists; includes extensive bibliographies.
- Bronn, H. G., et al.: Klassen und Ordnungen der Thies-Reichs. Letzgia and Beisdelberg, Winter 1874date. A voluminous work by various authors, published in parts, some old, some new, some as yet incomplete, which gives great attention to the anatomy of the various vertebrate groups as well as to classification and distribution.
- Kükenthal, W., and Krumbach, T., editors: Handbuch der Zoologie. Berlin and Leipzig, W. de Gruyter & Company, 1923—date. A work similar to the last in scope; incomplete, as yet.
- Grassé, P. P.: Traité de Zoologie, Anatomie, Systematique, Biologie, Vols. 1–17. Paris, Masson et Cie, 1948–1958. Not yet complete. Vol. 1X treats of lower chordates; vols. X–XVII of vertebrates.
- Goodrich, E. S.: Studies on the Structure and Development of Vertebrates. London, The Macmillan Company, 1930. A stimulating discussion of many anatomic problems by a first rate authority. Reprinted by Dover Publications, New York, 1958.

vertebrates.

Owen, R.: On the Anatomy of Vertebrates, 3 vols. London, Longmans, Green, 1866-1868, A classic.

full of original observations Cuvier, G.: Leçons d'Anatomie Comparée. 5 vols. Paris, 1805. The first great comparative anatomy. Young, I. Z.: The Life of Vertebrates, 2nd ed. London and New York, Oxford University Press, 1962. An excellent, group by group account, not only of structure but of life habits and functions of the

Marinelli, W., and Strenger, A.: Vergleichende Anatomie und Morphologie der Wirheltiere. Wien. Franz Deuticke, 1954, 1959. Parts so far issued treat of cyclostomes and Squalus.

Ihle, J. E. W., et al.: Vergleichende Anatomie der Wirbeltiere. Berlin, J. Springer, 1927. A substantial

volume on comparative anatomy by Dutch authors, translated into German. Böker, H.: Einführung in die vergleichende biologische Anatomie der Wirbeltiere. 2 vols. Jena. Gustav Fischer, 1935, 1937.

Romer, A. S.: The Vertebrate Story, Chicago, University of Chicago Press, 1959. An elementary account of vertebrate evolution.

Colbert, E. H.: Evolution of the Vertebrates. New York, Wiley, 1955.

Romer, A. S.: Vertebrate Paleontology. 2nd ed. Chicago, University of Chicago Press, 1945.

Piveteau, J.: Traité de Paléontologie. 8 vols. Paris, Masson et Cie, 1952-1958. A comprehensive work. five volumes of which treat of vertebrates. The volume on fishes not yet published. Thompson, D. W.: On Growth and Form, 2nd ed. Cambridge, England, Cambridge University Press,

1942. Nomina Anatomica, Revised by the International Anatomical Nomenclature Committee, Baltumore, Wil-

liams & Wilkins Company, 1956. Prosser, C. L., and Brown, F. A., Jr.: Comparative Animal Physiology. 2nd ed. Philadelphia, W. B. Saunders Company, 1961. Contains much data on physiology of vertebrates as a whole. (The data

of standard texts on human physiology such as the work next cited apply well to mammals but in a much lesser degree to other vertebrate groups.) Ruch, T. C., and Fulton, J. F.: Medical Physiology and Biophysics, (18th edition of Howell's Textbook

of Physiology) Philadelphia, W. B. Saunders Company, 1960. Buddenbrock, W. von: Vergleichende Physiologie. 4 vols. Basel, Birkhäusen, 1950–1956.

# CELLS AND TISSUES

Scott, G. G., and Kendall, J. L.: The Microscopic Anatomy of Vertebrates. 3rd ed. Philadelphia, Lea and Febiger, 1947.

Cole, C. A.: Comparative Histology, New York, Blakiston Company, 1955.

Krause, R.: Mikroskopische Anatomie der Wirheltiere. Berlin, W. de Gruyter & Company. 1923. Maximow, A., and Bloom, W.: A Textbook of Histology. 5th ed. Philadelphia, W. B. Saunders Com-

pany, 1948. This and the two following are representative histologies based on human material. LeGros Clark, W. E.: The Tissues of the Body. 2nd ed. London and New York, Oxford University Press.

1945 Windle, W. F.: Textbook of Histology. 3rd ed, New York, McGräw-Hill, 1960.

De Robertis, E. D. P., Nowinski, W. W., and Saez, F. A.: General Cytology. 3rd ed. Philadelphia, W. B. Saunders Company, 1960.

Baldwin, E.: An Introduction to Comparative Buchemistry, 3rd ed. Cambridge, England, Cambridge University Press, 1952.

#### EMBRYOLOGY

DeBeer, G. R.: Embryos and Ancestors. London and New York, Oxford University Press, 1951. Brachet, A., Daleq, A., and Gérard, P.: Traité d'Embryologie des Vertéhrés, 2nd ed. Paris, Masson et Cie. 1935.

Nelsen, O. E.: Comparative Embryology of Vertebrates. New York, Blakiston Company, 1953.

Hertwig, O., and others: Handbuch der vergleichenden und experimentellen Entwickelungslehre der Wubeltiere, 3 vols. Jena, Fischer, 1901-1906. A comprehensive, well illustrated work; out of date in certain aspects.

Kerr, J. G.: Text-Book of Embryology, Vol. II. Vertebrata with the Exception of Mammals. London, Macmillan Company, 1919.

Witschi, E.: Development of Vertebrates. Philadelphia, W. B. Saunders Company, 1956.

REFERENCES 445

Willier, B. H., Weiss, P. A., and Hamburger, V., editors: Analysis of Development. Philadelphia, W. B. Saunders Company, 1955.

Waddington, C. H.: Principles of Embryology. London, George Allen & Unwin, 1956.

Arey, L. B.: Developmental Anatomy. 6th ed. Philadelphia, W. B. Saunders Company, 1954. Primarily mammalian and human.

Hamilton, W. J., Boyd, J. D., and Mossman, H. W.: Human Embryology. 2nd ed. Cambridge, England, Helfer, 1952.

Starck, D.: Embryologie. Stuttgart, Thieme, 1955.

Patten, B. M.: Foundations of Embryology. New York, McGraw-Hill, 1958.

Patten, B. M.: Foundations of Employeegy, New York, McGraw-Hill, 1948.

Lillie, F. R.: Development of the Chick; revised and edited by H. L. Hamilton, New York, Holt, 1952. Patten, B. M.: Early Embryology of the Duck. 4th ed. New York, McGraw-Hill, 1951.

Waddington, C. H.: The Epigenetics of Birds. London, Cambridge University Press, 1952.

Romanoff, A. L.: The Avian Embryo. New York, The Macmillan Company, 1960.

Hörstadius, S.: The Neural Crest. London, Oxford University Press, 1950.

## SKIN

Schalfer, Jr. Die Haudrüßenorgane der Sügertiere. Berlin and Wien, Urban um Schwarzenberg, 1940.
Fox, L. D.: Animal Böcchrones and Structural Colours. London, Cambridge University Press, 1953.
DoSbanc, G.: The embryology of vertebrate pigment cells. Part I. Amphibia. Quart. Rev. Biol. 18:109–127, 1943. Part II. Birds, 19598–117, 1940.

Parker, G. H.: Animal Color Changes and their Neurohumors. London, Cambridge University Press, 1948

Lillic, F. R.: On the development of feathers. Biol. Rev. 17:247-266, 1942.

Paris, P.: Recherches sur la gland uropygienne des oiseaux. Arch. Zoologie Expérimental et Générale 53:132-276, 1914.

Harvey, E. N.: Bioluminescence, New York, Academic Press, 1952.

#### SKELETON

Reynolds, S. H.: The Vertebrate Skeleton. 2nd ed. Cambridge, 1913.

Gregory, W. K.: Evolution Emerging. 2 vols. New York, The Macmillan Company, 1951. Extremely valuable illustrations.

Kummer, B.: Bauprinzipien des Skelets. Stuttgart, Thieme, 1959.

Murray, P. D. F.: Bones, A study of the Development and Structure of the Vertebrate Skeleton. London, Cambridge University Press, 1936.

Haines, R. W.: The evolution of epiphyses and of endochondral bone. Biol. Rev. 17:267-292, 1942.
Gray, J.: How Animals Move. London, Cambridge University Press, 1953.

Goodrich, E. S.: On the scales of fish, living and extinct, and their importance in classification. Proc. Zool. Soc. London, 751-774, 1908.

Kerr, T.: The scales of primitive living actinopterygians. Proc. Zool. Soc. London 122:55–78, 1952.
Schmalhausen, J. J.: Zur Morphologie der unpaaren Flossen. Zischr. wissenschaftliche Zoologie 100: 509–587; 104:1–80, 1912-1913.

Goodrich, E. S.: On the dermal fin-rays of fishes—living and extinct. Quart. J. Microscopical Sc. 47: 465–522, 1904.

Williams, E. E.: Gadow's arcualia and the development of tetrapod vertebrae. Quart. Rev. Biol., 34:1–32, 1959.

Piiper, J.: On the evolution of the vertebral column in birds. Philos. Trans. Roy. Soc. London (B) 216: 285-351, 1928.

Westoll, T. S.: The Lateral Fin-fold Theory and the Pectoral Fins of Ostracoderms and Early Fishes. In Westoll, T. S., ed.: Studies on Fossil Vertebrates. London, University of London, 180-211, 1958. Gregory, W. K., and Raven, H. C.: Studies on the origin and early evolution of paired fins and limbs.

Ann. New York Acad. Sc. 42:273-360, 1944.

Parker, W. K.: A Monograph on the Structure and Development of the Shoulder Girdle and Sternum.

London, Ray Society, 1868.

Watson, D. M. S.: The evolution of the tetrapod shoulder girdle and fore-limb. J. Anat. 52:1-63, 1917.

Schaeffer, B.: The morphological and functional evolution of the tarsus in amphibians and reptiles. Bull. Am. Museum Natural Hist. 78:395–472, 1941.

Gregory, W. K., Miner, R. W., and Noble, G. K.: The carpus of Eryops and the primitive cheiroptery-gium. Bull. Am. Museum Natural Hist. 48:279-288, 1923.

Fisher, H. I.: Adaptations and comparative anatomy of the locomotor apparatus of New World vultures. Am. Midland Naturalist 35:545-727, 1946.

Berger, A. J.: The comparative functional morphology of the pectoral appendage in three genera of Guculidae, Am. Midland Naturalist 47:513-605, 1952.

Romer, A. S.: The Osteology of Reptiles. Chicago, University of Chicago Press, 1956.

Shufeldt, R. W.: Osteology of hirds. Bull. New York State Museum 130:5–381, 1909.

Flower, W. H.: An Introduction to the Osteology of the Mammalia. 3rd ed. London, The Macmillan Company, 1885, An old but useful little book. (Reissued by Dover Press, New York, 1962.)

Jayne, H.: Mammalian Anatomy. Part I. The Skeleton of the Cat. Philadelphia, Lippincott Company, 1896.

# SKULL

- DeBeer, G. R.: The Development of the Vertebrate Skull. London and New York, Oxford University Press, 1937. Publication preceded by a series of detailed papers on various forms by DeBeer and colleagues. Good bibliography.
- Parker, W. K. Structure and development of the skull. A long series of papers on the following forms: Ontrich, Food, Ram, Batrachia, Salmon, Pig. Uredeal, Tropidomota, Locertilia, Acipment, Lepidosteus, Edemata and Insectivora, Birds, Sharks and Skates, Grocdilia, Opisthocomus, in the following purmals Philos, Trans. Roy. Soc. Lendon 9, 10, 11, 13, 1875–1891; Tr. Linnean Soc. London, 200dgpt, 12, 11875–11880, 10bb usef illustrated and valuable.
- Gregory, W. K.: Fish skulls: A study of the evolution of natural mechanisms. Tr. Am. Philosophical Soc. 23:75–481, 1933.
- Schauinsland, H.: Beiträge zur Entwickelungsgeschichte und Anatomie der Wirbeltiere: Sphenodon, Callorhynchus, Chamaeleo, Zoologica (Stuttgart) 16:1-98, 1903.
- Gaupp, E.: Das Chondroeranium von Lacerta agilis. Anatomische Hefte (Arb.) 15:433-595, 1900.
  Peyer, B.: Die Entwicklung des Schädelskelettes von Vipera aspis. Morphologisches Jahrbuch 44:563-
- 621, 1912.
  Ration Steologie des Schlangenkopfes. Jenaische Ztschr. Naturwissenschaft 71:179–312, 1937.
  Brock, G. T.: On the development of the skull of Leptodeira hotamboia. Quart. J. Microscopical Sc. 73:
- 289-334, 1929.

  Bellairs, A. d'A.: The anterior brain-case and interorbital septum of Sauropsida with a consideration of
- the origin of snakes. J. Linnean Soc. London, Zoology, 41:482-512, 1949.

  Versluys, J.: Das Streptostylie-Problem und die Bewegungen im Schädel bei Sauropsiden. Zoologische
- Jahrbücher (Anat.), Supplement 15(2): 545-714, 1912.
- Jollie, M. T.: The head skeleton of the lizard. Acta Zoologica, 41:1-64, 1960.
  Lakjer, T.: Studien über die Gaumenregion bei Sauriern im Vergleich mit Anamniern und primitiven Saurossiden. Zoologische lährbücher 49:57-356, 1927.
- Hofer, H.: Neuere Untersuchungen zur Kopfmorphologie der Vögel. Basel, Acta 11th Congrès International d'Ornithologie 104–137, 1955.
- Crompton, A. W.: The development of the chondrocranium of Spheniscus demersus with special reference to the columella auris of birds. Acta Zoologica 34:71–146, 1953.
- ence to the columella auris of birds. Acta Zoologica 34:71–140, 1953.
  Lang, C.: Das Cranium der Ratiten mit besonderer Berücksichtigung von Struthio camelus. Ztschr. wissenschaftliche Zoologie 159:165–224, 1956.
- Jollie, M. T.: The head skeleton of the chicken and remarks on the anatomy of this region in other birds. J. Morphol. 100:389-436, 1957.
- Starck, D.: Zur Morphologie des Primordialeraniums von Manis javanica Desm. Morphologisches Jahrbuch 86:1-122, 1941. One of a series of mammal skull studies by Starck and his students.
- Kampen, P. N. van: Die Tympanalgegend des Säugetierschädels. Morphologisches Jahrbuch, 34:321–722, 1905.

## MUSCLES

- Fisher, H. I., and Goodman, D. C.: The Myology of the Whooping Crane, Grus americana. Illinois Biological Monographs, 24, no. 2, 1955.
- Shufeldt, R. W.: The Myology of the Rayen, New York, Macmillan Company, 1890.
- Maurer, F.: Die Entwicklung der ventralen Rumpfmuskulatur bei Reptilien. Morphologisches Jahrbuch 26:1–60, 1898.
- Straus, W. L., and Rawles, M. E.: An experimental study of the origin of the trunk musculature and ribs in the chick. Am. J. Anat. 92:471-510, 1953.
- Gilbert, P. W.: The origin and development of the human extrinsic ocular muscles. Contrib. Embryol. 36:59–78, 1957.
- Braus, H.: Die Muskeln und Nerven der Ceratodusflosse. Semon's Zoologische Forschungsreisen in Australien 1:137–300, 1901.
- Scwertzoff, A. N.: Studien über die Entwickelung der Muskeln, Nerven und des Skeletts der Extremitäten der niederen Tetrapoda, Bull. Soc. Impériale Naturalistes Moscou (n.s.) 21:1–430, 1907.
- Romer, A. S.: The development of tetrapod limb musculature—the shoulder region of Lacerta. J. Morphol. 74:1-41, 1944.
- Romer, A. S.: The development of the thigh musculature of the chick. J. Morphol. 43:347–385, 1927.
  Fürbringer, M.: Zur vergleichenden Anatomie des Brastschulterapparates und der Schultermuskeln.
  Jenaische Zischr. Naturwissenschaft 36:289–736. 1902. Morphologisches Jahrbuch J. 1875.
- 7, 1873; 8, 1874; 34, 1902.
  Sy. M.: Funktionell-anatomische Untersuchungen am Vogelftügel. J. Ornithologie 84:199–296, 1936.
  Hudson, G. E.: Studies on the muscles of the pelvic appendage in birds. Am. Midland Naturalist 18:1-
- 108, 1937.
  Howell, A. B.: Morohogenesis of the shoulder architecture: Aves. Auk 54:363–375, 1937.
- Edgeworth, F. H.: The Cranial Muscles of Vertebrates. London, The Macmillan Company, 1935.

  Druner, L.: Zungenbein, Kiemenbogen und Kehlkoof-Muskeln der Urodelen, Zoologische Jahrbücher.
- Abteilung für Anatomie und Ontogenie der Tiere 15:435–622; 19:361–690, 1902–1904. Lakjer, T.: Studien über die Trigeminus-versorgte Kaumuskulatur der Sauropsiden. Copenhagen, C. A.
- Reitzel, 1926.
  Haas, G.: Die Kiefermuskulatur und die Schädelmechanik der Schlangen in vergleichender Darstellung.
  Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere 53:127–198, 1931. See
- also ibid. 52:1–218, 1930.
  Starck, D., and Barnikol, A.: Beitrage zur Morphologie der Trigeminusmuskulatur der Vögel (besonders
- der Accipitres, Cathartidae, Striges und Anseres). Morphologisches Jahrbuch 94:1-64, 1954.
  Hofer, H.: Zur Morphologie der Kiefermuskulatur der Vögel. Zoologische Jahrbücher 70:427-556, 1950.
- Cheng, C. C.: The development of the shoulder region of the opossum, Didelphys virginiana, with special reference to the musculature. J. Morphol. 97:415-471, 1955.
- Grandfert, H.: Electric fishes. Scientific American 203:115-120, 1960.

# CELOM

- Butler, G. W.: On the subdivision of the body-cavity in lizards, crocodiles, and birds. Proc. Zool. Soc. London 452-474, 1889; snakes, 477-498, 1892.
- Mall, F. P.: Development of the human coelom. J. Morphol. 12:395-453, 1897.
- Keith, A.: The nature of the mammalian diaphragm and pleural cavities. J. Anat. Physiol. 39:243–284, 1905.
- Wells, L. J.: Development of the human diaphragm and pleural sacs. Carnegie Inst. Washington, Contrib. Embryol. 35:107-134, 1954.

#### MOUTH AND PHARYNX

- Sonntag, C. F.: The comparative automy of the tongues of the Mammalia. Proc. Zool. Soc. London, 1920, 115-129; 1921, 1-29, 277-322, 497-521, 741-755, 757-767; 1922, 639-657; 1923, 129-153, 515-529, 1924, 725-741, 743-755.
- Tims, H. W., and Henry, C. B.: Tomes' Dental Anatomy. New York, The Macmillan Company, 1923.
  Owen, R.: Odontography—A Treatise on the Comparative Anatomy of the Teeth. London, Hippolyte Builliere, 1840. Despite its antiquity, a valuable comprehensive account.
- Scott, J. H., and Symons, N. B. B.: Introduction to Dental Anatomy. Edinburgh and London, E. and S. Livingstone, 1952.

Appelbaum, E.: Enamel of sharks teeth, J. Dent. Res. 21:251-257, 1942. Edmund, A. G.: Tooth Replacement Phenomena in the Lower Vertebrates. Contribution 52, Life Sci-

ences Division, Royal Ontario Museum, Toronto, 1960. Gregory, W. K.: A half century of trituberculy. The Cope-Osborn theory of dental evolution, with a revised summary of molar evolution from fish to man. Proc. Am. Philosophical Soc. 73:169-317, 1934. Woskoboinikoff, M.: Der Apparat der Kiemenatmung bei den Fischen. Zoologische Jahrbücher, Abteilung

für Anatomie und Ontogenie der Tiere 55:315-488, 1932. Copeland, D. E.: The cytological basis of chloride transfer in the gill of Fundulus heteroclitus. J. Morphol. 82:201-227, 1948; 87:369-380, 1950. Adams, W. E.: The cervical region of the Lacertilia. J. Anat. 74:57-71, 1939.

Klapper, C. E.: The development of the pharynx of the guinea pig with special emphasis on the fate of the ultimobranchial body. Am. J. Anat. 79:361-397, 1946.

Jones, F. R. H., and Marshall, N. B.: The structure and functions of the teleostean swimbladder. Biol. Rev. 28:16-83, 1953.

Rauther, M.: Zur vergleichenden Anatomie der Schwimmblase der Fische. Ergeb. Zoologie 5:1-66, 1922. Ballantyne, F. M.: Air bladder and lungs; a contribution to the morphology of the air bladder of fish, Tr. Roy. Soc. Edinburgh 55:371–394, 1927.

Müller, B.: The air sacs of the pigeon. Smithsonian Miscellaneous Collections 1:365-414, 1908. Locy, W. A., and Larsell, O.: The embryology of the birds' lung. Am. J. Anat. 19:447-501, 1916.

Huntington, G. S.: A critique of theories of pulmonary evolution in the Mammalia. Am. J. Anat. 27: 99-201, 1920.

#### DIGESTIVE SYSTEM

Slijper, E. J.: Die physiologische Anatomie der Verdauungsorgane bei den Vertebraten, Tabulae Biologicae 21:1-81, 1946.

Peterson, H.: Beiträge zur Kenntniss des Baues und der Entwickelung des Selachierdarmes. Jenaische Ztschr. Naturwissenschaft 43:619-652; 44:123-148, 1908.

Jacobshagen, E.: Untersuchungen über das Darmsystem der Fische und Dipnoer. 11. Jenaische Ztschr. Naturwissenschaft 49:373-810, 1913.

Hopkins, G. S.: On the enteron of American ganoids. J. Morphol. 11:411-442, 1895.

Greene, C. W.: Anatomy and histology of the alimentary tract of the king salmon. Bull. U. S. Burcau Fisheries, 32:73-100, 1912. Blake, I. H.: Studies on the comparative histology of the digestive tube of certain teleost fishes. J.

Morphol. 50:39-70, 1930; 60:77-102, 1936. Mitchell, P. C.: On the intestinal tract of birds; with remarks on the valuation and nomenclature of zoo-

logical characters. Tr. Linnean Soc. London, Zoology 8:173-275, 1901. Calhoun, M. L.: Microscopic Anatomy of the Digestive System of the Chicken. Ames, Iowa State

College Press, 1954. Pernkopf, E.: Beiträge zur vergleichende Anatomie des vertebraten Magens, Ztschr. Anat. 91:329-390.

Hirsch, G. C.: Magenlose Fische, Zoologischer Anzeiger, Ergänzungsband 145:302-326, 1950.

Cornselius, C.: Morphologie, Histologie und Embryologie des Muskelmagens der Vögel. Morphologisches Jahrbuch 54:507-559, 1925.

Kaden, L.; Über Epithel und Drüsen des Vogelschlunds. Zoologische Jahrbücher. Abteilung für Anatomie und Ontogenie der Tiere. 61:421-466, 1936.

Elias, H.: Liver morphology, Biol. Rev. 30:263-310, 1955.

Gorham, F. W., and Ivy, A. C.: General function of the gall bladder from the evolutionary standpoint. Field Museum of Natural History, Zoology Series, 22:159–213, 1938.

Hill, W. C. O.: A comparative study of the pancreas. Proc. Zool. Soc. London 581-631, 1926.

# URINARY AND REPRODUCTIVE SYSTEMS

Fraser, E. A.: The development of the vertebrate excretory system. Biol. Rev. 25:159-187, 1950. Conel, J. L.: The urogenital system of myxinoids. J. Morphol. 29:75-164, 1917.

Borcea, J.: Recherches sur le système uro-genital des elasmobranchs. Arch. Zoologie expérimentale et générale (4) 4:199-484, 1906.

REFERENCES 449

Kempton, R. T.: Studies on the elasmobranch kidney. J. Morphol. 73:247-263, 1943; Biol. Bull. 104: 45-56, 1953.
Kimdahl, M.: Zur Entwicklung der Exkretionsorgane von Dipnoërn und Amphibien. Acta Zoologica, 19:

Kimdahl, M.: Zur Entwicklung der Exkretionsorgane von Dipnoërn und Amphibien. Acta Zoologica, 19 1-190, 1938.

Gray, P.: The development of the amphibian kidney. Quart. J. Microscopical Sc. 73:507-546, 1930; 75:425-466, 1932; 78:445-473, 1936.

Semon, R.: Studien über den Bauplan des Urogenitalsystems der Wirheltiere. Dargelegt an der Entwickelung dieses organsystems bei Ichthyophis glutinosus. Jenaische Ztschr. Naturwissenschaft, 26: 80–203, 1892.

Buchanan, G., and Fraser, E. A.: The development of the urinogenital system in the Marsupialia with special reference to Trichosurus vulpecula. Part 1. J. Anat. 53:35–95, 1918.

Smith, H. W.: The Kidney. London and New York, Oxford University Press, 1951.

Huber, G. C.: On the morphology of the renal tubules of vertebrates. Anat. Rec. 13:305-339, 1917.
Edwards, J. G.: Studies on aglomerular and glomerular kidneys. Am. J. Anat. 42:75-108, 1928, Anat. Rec. 44:15-28, 1929.

Smith, H. W.: Water regulation and its evolution in fishes. Quart. Rev. Biol. 7:1-26, 1932.

Smith, H. W.: From Fish to Philosopher. Boston, Little, Brown and Company, 1953. Vertebrate evolution with kidney evolution as the leitmotif.

Swift, C. H.: Origin and early history of primordial germ cells in the chick. Am. J. Anat. 15:483-516, 1914.

Everett, H. B.: The present status of the germ-cell problem in vertebrates. Biol. Rev. 20:45-55, 1945. Witschi, E.: Migration of the germ cells of human embryos from the yolk sac to the primitive gonadal

folds. Carnegie Inst. Washington, Contrib. Embryol. 32:67–80. 1948.
Maschkowerd, Ja.: Zur Phylogenie der Gesehlechtsdrüsen und der Gesehlechtsausfuhrgänge bei den Vertebrata auf Grund von Forschungen betreffend die Entwicklung des Mesonephros und der Gesehlechtsorane bei den Acienserfeine, Salmoniden und Amphibien. Zoologische Jahrückler. Abteilung für

Anatomie und Onlogenie der Tiere 59:1–68, 201–276, 1934–35.

Moore, C. R.: The biology of the mammalian testis and scrotum. Quart. Rev. Biol. 1:4–50, 1926.

Boyden, E. A.: The development of the closea in birds. Am. J. Anat. 30:163–201, 1922. Leigh-Sharper, W. H.: The comparative morphology of the secondary sexual characters of elasmobranch fishes. J. Morphol. 34:245–265, 35:359–380, 36:221–243; 42:307–308, 1920–1926.

# CIRCULATORY SYSTEM

Jordan, H. E.: The evolution of blood-forming tissues. Quart. Rev. Biol. 8:58-76, 1933.
Chèvremont, M.: Le système histiocytaire ou réticulo-endothélial. Biol. Rev. 23:267-295, 1948.

Krogh, A.: The Anatomy and Physiology of Capillaries. New Haven, Yale University Press, 1929.Drinker, C. K., and Jaffey, J. M.: Lymphatics, Lymph and Lymphoid Tissue. Cambridge, Harvard Uni-

versity Press, 1941.

Versity Press, 1951.

O'Donoghue, C. H., and Abbott, E.: The blood-vascular system of the spiny dogfish, Squalus acanthias

Linn., and Squalus sucklii Gill. Tr. Roy. Soc. Edinburgh, 55:283-890, 1928.
Robertson, J. L.: The development of the heart and vascular system of Lepidosiren paradoxa. Quart. J.

Microscopical Sc. 59:53–132, 1913.
O'Donoghue, C. H.: The blood-vascular system of the tuatara, Sphenodon punctatus. Philos. Tr. Roy. Soc. Londor (Bg 210:175–252, 1920.

O'Donoghue, C. H.: The circulatory system of the common grass snake (Tropidonotus natrix). Proc. Zool. Soc. London 612-647, 1912.

Hochstetter, T.: Beiträge zur Anatomie und Entwickelungsgeschichte des Blutgefässsystemes der Krokodile. Voeltzkow, A., Reise in Ostafrika, 4:1–139, 1906.

Hill, W. C. O.: The blood-vascular system of Tarsius. Proc. Zool. Soc. London, 123:655-692, 1953.
Heuser, C. H.: The branchial vessels and their derivatives in the pig. Carnegie Inst. Washington, Con-

trib. Embryol. 15:121–139, 1923.
Davis, D. D., and Storey, H. E.: The carotid circulation in the domestic cat. Publications, Field Museum of Natural History, Zoology, 28:5–47, 1943.

Reagan, F. P.: A century of study upon the development of the eutherian vena cava inferior. Quart. Rev. Biol. 4:179-212, 1929.

Butler, E. G.: The relative role played by the embryonic veins in the development of the mammalian vena cava posterior. Am. J. Anat. 39:267-353, 1927.

Barnett, C. H., Harrison, R. J., and Tomlinson, J. D. W.: Variations in the venous systems of mammals. Biol. Rev. 33:442-487, 1958. Padget, D. H.: The development of the cranial venous system in man, from the viewpoint of comparative anatomy. Carnegie Inst. Washington, Contrib. Embryol. 36:79-140, 1957. Grei), A.: Beiträge zur vergleichenden Anatomie und Entwicklungsgeschichte des Herzens und des Trun-

188, 1946. Benninghoff, A.: Beiträge zur vergleichenden Anatomie und Entwicklungsgeschlichte des Amphibien-

Davies, F., and Francis, E. T. B.: The conducting system of the vertebrate heart. Biol. Rev. 21:173-

cus arteriosus der Wirheltiere, Morphologisches Jahrbuch 31:123-310, 1903.

herzens und zur Phylogenie des Reizleitungssystems. Morphologisches Jahrbuch 51:354-412, 1921. Kern, A.: Das Vogelherz. Morphologisches Jahrbuch 56:264-315, 1926.

## SENSE ORGANS

Parker, G. H.: Smell, Taste, and Allied Senses in the Vertebrates. Philadelphia, Lippincott Company,

Baradi, A. F., and Bourne, G. H.: Gustatory and olfactory epithelia. Internat. Rev. Cytol. 2:289-330. 1053

Noble, G. K., and Schmidt, A.: The structure and function of the facial and labial pits of snakes. Proc. Am. Philosophical Soc. 77:263-288, 1937.

Pumphrey, R. J.: The sense organs of birds. Ibis, 90:171-199, 1948; Annual report of the Smithsonian Institution 305-330, 1948.

Allison, A. C.: The morphology of the olfactory system in vertebrates. Biol. Rev. 28:195-244, 1953. Burne, R. H.: The anatomy of the olfactory organ of teleostean fishes. Proc. Zool. Soc. London 610-662, 1909.

Parsons, T. S.: Studies on the comparative embryology of the reptilian nose. Bulletin, Museum of Comparative Zoology, Harvard, 120:104-277, 1959.

Fånge, R., Schmidt-Nielsen, K., and Osaki, H.: The salt gland of the herring gull. Biol. Bull. 115:162-171, 1958.

Walls, G. L.: The vertebrate eve and its adaptive radiation. Cranbrook Institute of Science, Bulletin No. 19, 1942.

Rochon-Duvigneaud, A.: Les Yeux et la Vision des Vertébrés. Paris, Masson et Cie, 1943.

Polyak, S.: The Vertebrate Visual System. Chicago, University of Chicago Press, 1958.

Detweiler, S. R.: Vertebrate Photoreceptors. New York, The Macmillan Company, 1943. Bellairs, A. d'A., and Boyd, J. D.: The lachrymal apparatus in lizards and snakes. Proc. Zool. Soc. Lon-

don 117:81-101, 1947; 120:269-309, 1950. Wright, M. E.: The lateral line system of sense organs. Quart. Rev. Biol. 26:264-280, 1951.

Dijkgraaf, S.: Bau und Funktionen der Seitenorgane und des Ohrlabyrinths der Fische. Experientia 8:

205-216, 1952. Lowenstein, O.: The equilibrium function of the vertebrate labyrinth. Biol. Rev. 11:113–145, 1936.

Werner, S. C.: Das Gehörorgan der Wirheltiere und des Menschen. Leipzig, George Thieme, 1960. Retzius, G.: Das Gehörorgan der Wirbelthiere. Morphologisch-histologische Studien. 2 vols. Stockholm,

Chranilov, N. S.: Beiträge zur Kenntniss der Weber'schen Apparates der Ostariophysi. Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere, 49:501-597, 1927; 51:323-462, 1929.

Reed, H. D.: The morphology of the sound-transmitting apparatus in caudate Amphibia. J. Morphol. 33: 325-375, 1920. Versluys, J.: Die mittlere und äussere Ohrsphäre der Lacertilia und Rhynchocephalia. Zoologische Jahr-

bücher, Abteilung für Anatomie und Ontogenie der Tiere, 12:161-406, 1898. See also Ibid. 18: 107-188, 1902.

Gaupp, E.: Die Reichertsche Theorie (Hammer- Amboss- und Kieferfrage). Arch. Anat. Physiol. Supplement V:1-417, 1913. On evolution of middle ear ossicles.

#### NERVOUS SYSTEM

Kappers, C. U. A., Huber, G. C., and Crosby, E. C.: The Comparative Anatomy of the Nervous System of Vertebrates, Including Man. 2 vols. New York, The Macmillan Company, 1936. A mine of information on comparative neurology, but difficult to work for one not a neurologist.

Kappers, C. U. A.: The Evolution of the Nervous System in Invertebrates. Vertebrates and Man. Haarlem, Erven F. Bohn, 1929.

Herrick, C. J.: An Introduction to Neurology. 5th ed. Philadelphia, W. B. Saunders Company, 1931.

REFERENCES 451

Papez, J. W.: Comparative Neurology. New York, Thomas Y. Crowell Company, 1929. (Reprinted 1961.) Johnston, J. B.: The Nervous System of Vertebrates. Philadelphia, P. Blakiston's Son and Company, 1006.

Detweiler, S. R.: Neuroembryology. New York, The Macmillan Company, 1936.

Bullock, T. H.: The anatomical organization of the nervous system of Enteropneusta. Quart. J. Microscopical Sc. 86:55-111, 1945.

Silén, L.: On the nervous system of Glossobalanus marginatus Meck. Acta Zoologica 31:149–175, 1950.
Weiss, P. A.: In vitro experiments on the factors determining the course of the outgrowing nerve fiber.
J. Exper. Zool. 68:393–448, 1934.

Herrick, C. J.: The doctrine of nerve components and some of its applications. J. Comp. Neurol. 13: 301–312, 1903.

Franz, V.: Nervensystem der Akranier. Jenaische Ztschr. Naturwissenschaft 59:401–526, 1923.

Tretjakoff, D.: Das periphere Nervensystem des Flussneunauges. Ztschr. wissenschaftliche Zoologie, 129:359–952, 1927.

Goodrich, E. S.: On the spinal nerves of the Myxinoidea. Quart. J. Microscopical Sc. 80:153-158, 1937. Lindstrom, T.: On the cranial nerves of the cyclostomes with special reference to the N. trigeminus. Acta Zoologica 39:315-458, 1949.

Herrick, C. J.: The cranial nerves of the bony fishes. J. Comp. Neurol. 9:153–455, 1899; cf. also 10: 265–322, 1900; 11:177–249, 1901.

Norris, H. W.: Cranial nerves of Siren lacertina. J. Morphol. 24:245-338, 1913.

Watkinson, G. B.: The cranial nerves of Varanus bivittatus. Morphologisches Jahrbuch 35:450-472, 1906.

Willard, W. A.: The cranial nerves of Anolis carolinensis. Bulletin, Museum of Comparative Zoology, Harvard 59:17-116, 1915.

Mitchell, G. A. G.: Anatomy of the Autonomic Nervous System. Edinburgh and London, E. and S. Livingstone, Ltd., 1953.

Nicol, J. A. C.: Autonomic nervous systems in lower chordates. Biol. Rev. 27:1-49, 1952.

Campenhout, E. van: Historical survey of the development of the sympathetic nervous system. Quart. Rev. Biol. 5:23-50, 217-234, 1930.

Yntema, C. L., and Hammond, W. S.: The development of the autonomic nervous system. Biol. Rev. 22: 344–359, 1947.

Bocke, J.: The autonomic (enteric) nervous system of Amphioxus lanceolatus. Quart. J. Microscopical Sc. 77:623-658, 1935.
Johnels, A. G.: On the peripheral autonomic system of the trunk region of Lampetra planeri. Acta Zoo-

logica 37:251-285, 1956. Young, J. Z.: The autonomic system of selachians. Quart. J. Microscopical Sc. 75:571-624, 1933.

Young, J. Z.: On the autonomic nervous system of the teleostean fish, Uranoscopus scaher. Quart. J. Microscopical Sc. 74:492–525, 1931.
Weed, L. W.: The development of the cerebro-spinal spaces in pig and in man. Carnegie Inst. Washington,

Weed, L. W.: The development of the extensiv-spinal spaces in pig and in man. Carnegor inst. Washington Contrib. Embryol. 5:3—116, 1917.
Stefanelli, A.: The mauthnerian apparatus in the Ichthyopsida. Quart. Rev. Biol. 21:17–34, 1951.

Herrick, C. J.: The Brain of the Tiger Salamander. Chicago, University of Chicago Press, 1948.

Norris, H. W., and Hughes, S. P.: The cranial, occipital and anterior spinal nerves of the dogfish. J. Comp. Neurol. 31:293-395, 1920.

Portmann, A.: Études sur la cérebralisation chez les oiseaux. Alauda 14:2-20, 1946; 15:1-15, 1947.
Herrick, C. J.: Brains of Rats and Men. Chicago, University of Chicago Press, 1926.

Krieg, W. J. S.: Functional Neuroanatomy. Philadelphia, Blakiston Company, 1942.

Larsell, O.: The development of the cerebellum in man in relation to its comparative anatomy. J. Comp. Neurol. 87:85-129, 1947.

# ENDOCRINE ORGANS

Turner, C. D.: General Endocrinology. 2nd ed. Philadelphia, W. B. Saunders Company, 1960.
Gorbman, A., editor: Comparative Endocrinology. New York, John Wiley and Sons, 1959.

Pickford, G. E., Palay, S. L., Chambers, H. A., and Atz, E. H.: Fish endocrinology. Bulletin of the Bingham Occanographic Collection 14:1-16, 1953.

Green, J. D.: The comparative anatomy of the hypophysis, with special reference to its blood supply and innervation. Am. J. Anat. 88:225–311, 1951.
Fields, W. S., Guillemin, R., and Carton, C. A., editors: Hypothalamic-hypophysial Interrelationships.

A Symposium. Houston, Baylor University College of Medicine, 1956.

Bargmann, W.: The neurosecretory system of the diencephalon. Endeavour 19:125–133, 1960.

282-316, 1949.

- Lynn, G. W., and Wachowski, H. E.: The thyroid gland and its functions in cold-blooded vertebrates. Quart. Rev. Biol. 26:123-168, 1951. Goldsmith, E. D.: Phylogeny of the thyroid: descriptive and experimental. Ann. New York Acad. Sc. 50:
- anatomisches Forschung 34:485-533, 1933.
- Boyd, J. D.: The development of the thyroid and parathyroid glands and the thymus. Ann. Roy. Coll. Surgeons England 7:455-471, 1950. Watzka, M.: Vergleichende Untersuchungen über den ultimobranchialen Körper. Ztschr. mikroscopisch-
- Marshall, F. H. A.: The Physiology of Reproduction, London, Longmans, Green, 1960.

# LOWER CHORDATES

- Grassé, P.-P., editor: Traité de Zoologie. Tome XI. Échinodermes-Stomocordés- Procordés. Paris, Masson et Cie, 1948. Contains a comprehensive account of lower chordates by Dawydoff, Brien, Drach, and
- Garstang, W.: The morphology of Tunicata. Quart. J. Microscopical Sc. 72:51-187, 1928.
- Franz, V.: Morphologie der Acranier. Ergebn. Anat. u. Entwicklungsgeschichte 27:464-692, 1927. Willey, A.: Amphioxus and the Ancestry of Vertebrates. New York, Columbia University, 1894.

#### FISHES

- Dean, B.: A Bibliography of Fishes. 3 vols. New York, American Museum of Natural History, 1916-1923.
- Berg, L. S.: Classification of Fishes, Both Recent and Fossil. Ann Arbor, Edwards Bros., 1947. A translation of a Russian original. A new edition in Russian published in 1949.
- Goodrich, E. S.: A Treatise on Zoology, edited by E. Ray Lankester. Part 1X. Vertebrata Craniata, Fascicule I. "Cyclostomes and Fishes." London, The Macmillan Company, 1909. A mine of data on fish anatomy; badly indexed, however.
- Norman, J. R.: A History of Fishes. 3rd ed. London, Ernest Benn, Ltd., 1947. Life history, habits, and so on, as well as structure.
- Bigelow, H. B., and Schroeder, W. C., editors: Fishes of the Western North Atlantic. New Haven, Sears Foundation for Marine Research, 1948. Designed as a comprehensive account of marine fishes. The first two volumes mainly devoted to sharks and rays.
- Moy-Thomas, J. A.: Palaeozoic Fishes. London, Methuen and Co., Ltd., 1939.
- Romer, A. S.: The early evolution of fishes, Quart. Rev. Biol. 21:33-69, 1946.
- Brown, M. E.: The Physiology of Fishes. 2 vols. New York. Academic Press, 1957. Despite the limitation of the title, gives in the main a comprehensive account of fish biology and anatomy.
- Breder, C. M.: The locomotion of fishes. Zoologica (New York) 4:159-297, 1926.
- Allis, E. P. Jr.: The cranial muscles and cranial and first spinal nerves in Amia calva. J. Morphol. 12: 487-808, 1897. This and the following works by Allis are well-illustrated accounts of cranial anatomv.
- Allis, E. P. Jr.: The skull and cranial and first spinal muscles and nerves in Scomber scomber. J. Morphol. 18:45-328, 1903,
- Allis, E. P. Ir.: The cranial anatomy of the mail-cheeked fishes. Zoologica (Stuttgart) 22:1–219, 1909.
- Allis, E. P. Jr.: Cranial anatomy of Polypterus. J. Anat. 56:189-294, 1922. Allis, E. P. Jr.: The cranial anatomy of Chlamydoselachus anguineus. Acta Zoologica 4:123-221, 1923.
- Cole, F. J.: A monograph on the general morphology of the myxinoid fishes, based on a study of Myxine. Tr. Roy. Soc. Edinburgh, 49:293–344, 1913.
- Daniel, J. F.: The Elasmobranch Fishes. 3rd ed. Berkeley, University of California Press, 1934. Shark anatomy.
- Dean, B.: Chimaeroid fishes. Carnegie Institution of Washington, Publication 32, 1906. Millot, J.: Le troisième coelacanthe. Le Naturaliste Malagache, 1er Supplement, 1954. Superficial struc-
- tures of Latimeria.
- Millot, J., and Anthony, J.: Anatomie de Latimeria chalumnae. 1. Squelette, Muscles et Formations de Soutien. Paris, Centre National de la Recherche Scientifique, 1958. The first of a series of anatomical monographs on this interesting animal.
- Greil, A.: Entwickelungsgeschichte des Kopfes und des Blutgefässsystems von Ceratodus forstern. Semon's Zoologische Forschungsreise in Australien 1:661-1492, 1908-1913.

#### AMPHIBIA

Noble, G. K.: The Biology of the Amphibia. New York, McGraw-Hill Book Company, Inc., 1931; reprinted by Dover Publications, New York, 1954.

Francis, E. T. B.: The Anatomy of the Salamander. London and New York, Oxford University Press, 1934.

Ecker, A., Wiedersheim, R., and Gaupp, E.: Anatomie des Frosches. 3 vols., 2nd ed. Braunschweig, Friedrich Viewig und Sohn, 1888–1904. A thorough account of frog anatomy, which has passed through the hands of three successive authors.

Holmes, S. J.: The Biology of the Frog. 4th ed. New York, Macmillan Company, 1927.
Wiedersheim, R.: Die Anatomie der Gymnophionen. Jena, Gustav Fischer, 1879.

Romer, A. S.: Review of the Labyrinthodontia. Bulletin, Museum of Comparative Zoology, Harvard, 99: 1-368, 1947.

#### REPTILES

Bellairs, A. d'A.: Reptiles. London, Hutchinson's University Library, 1957.

Pope, C. H.: The Reptile World. New York, Alfred A. Knopf, 1955.

Ditmars, R. L.: Reptiles of the World. New York, The Macmillan Company, 1933.

Oliver, J. A.: The Natural History of North American Amphibians and Reptiles. Princeton, Princeton University Press, 1955.

Carr, A.: Handbook of Turtles. Ithaca, Cornell University Press, 1952.

Bellairs, A. d'A., and Underwood, G.: The origin of snakes. Biol. Rev. 26:193-237, 1951.
Reese, A. M.: The Alligator and its Allies. New York, G. P. Putnam Sons, 1915.

Colbert, E. H.: Dinosaurs, Their Discovery and Their World. New York, E. P. Dutton and Company, 1961.

Williston, S. W.: Water Reptiles of the Past and Present. Chicago, University of Chicago Press, 1914.

#### BIRDS

- Pycraft, W. P.: A History of Birds. London, Methuen and Company, 1910. Includes anatomy. Thompson, J. A.: The Biology of Birds. London, The Macmillan Company, 1923.
- Newton, A., and Gadow, H.: A Dictionary of Birds. London, Adam and Charles Black, 1893–1896.
- Strong, R. M.: A bibliography of birds. Publication, Field Museum of Natural History, Zoology, 25: 1939-1959.
- Marshall, A. J.: Biology and Comparative Physiology of Birds. 2 vols. New York, Academic Press, 1960–1961.
- Wolfson, A., editor: Recent Studies in Avian Biology. Urbana, University of Illinois Press, 1955.
- Bradley, O. C.: The Structure of the Fowl. 2nd ed. London, Oliver and Boyd, Ltd., 1938.

  Chamberlain, I. W.: Atlas of Avian Anatomy, East Lansing, Michigan State College, Agricultural Ex-
- Chamberlain, L. W.: Atlas of Avian Anatomy. East Lansing, Michigan State College, Agricultural Experiment Station, 1943.
- Heilmann, G.: The Origin of Birds. New York, D. Appleton-Century Company, 1926.Holmgren, N.: Studies on the phylogeny of birds. Acta Zoologica 36:243–328, 1955.
- Fürbringer, M.: Untersuchungen zur Morphologie und Systematik der Vögel. Zugleich ein Beitrag zur Anatomie des Stütz- und Bewegungsorgane. 2 vols. Amsterdam and Jena, Gustav Fischer, 1888. Old
- but still basic work, including excellent comparative anatomical data.

  Boas, J. E. V.: Biologisch-anatomische Studien über den Hals der Vögel. Kongelige Danske Videnskabernes Selskab, naturvidenskabelig og mathematisk Afdeling, Series 9, 1:101-222, 1929.
- Webb, M.: The ontogeny of the cranial bones, cranial peripheral and cranial parasympathetic nerves, together with a study of the visceral muscles of Struthio. Acta Zoologica 38:81–203, 1957.
- Groebbels, F.: Der Vogel. Volume 1. Atmungswelt und Nahrungswelt. Berlin, Gebrüder Borntraeger, 1932. Volume 2. Geschlecht und Fortoffanzuns. 1937.
- De Beer, G.: Archaeopteryx lithographica. London, British Museum (Natural History), 1954.

#### MAMMALS

Simpson, G. G.: The principles of classification and a classification of mammals. Bulletin, American Museum of Natural History 88:1-350, 1945.

Weber, M., Burlet, H. M. de, and Abel, O.: Die Säugetiere. 2 vols., 2nd ed. Jena, Gustav Fischer, 1927-1928. A standard work on mammalian anatomy and classification.

Flower, W. H., and Lydekker, R.: An Introduction to the Study of Mammals, Living and Extract. London, Adam and Charles Black, 1891. Old, but still useful.

Bourlière, F.: The Natural History of Mammals. New York, Alfred A. Knopf, 1954.

Young, J. Z.: The Life of Mammals. London, Oxford University Press, 195

Sisson, S., and Grossman, J. D.: The Anatomy of the Domestic Animals. 3rd ed. Philadelphia, W. B. Saunders Company, 1938. A comprehensive account of horse anatomy; ox, sheep, pig, and dog are covered more briefly.

Davison, A., and Stromsten, F. A.: Mammalian Anatomy, with Special Reference to the Cat. 7th ed. Philadelphia, P. Blakiston's Son and Company, 1937.

Reighard, J. E., and Jennings, H. S.: Anatomy of the Cat. 3rd ed. New York, Henry Holt and Company. Inc., 1935.

Bradley, O. C., and Grahame, T.: Topographical Anatomy of the Dog. 5th ed. New York, The Macmillan Company, 1943.

Baum, H., and Zietzschmann, O.: Handbuch der Anatomie des Hundes. Berlin, P. Parev, 1936.

Greene, E. C.: Anatomy of the rat. Tr. Am. Philosophical Soc. (n.s.) 27:1-370, 1935.

Howell, A. B.: Anatomy of the Wood Rat. Baltimore, Williams and Wilkins Company, 1926. Gerhardt, U.: Das Kaninchen, Leipzig, H. E. Ziegler and R. Woltereck, 1909.

Ellerman, J. R.: The Families and Genera of Living Rodents. 3 vols. London, British Museum (Natural

History), 1940-1949. Bensley, B. A., and Craigie, E. H.: Practical Anatomy of the Rabbit. 8th ed. Philadelphia, Blakiston

Company, 1948. Howell, A. B.: Aquatic Mammals. Springfield, Illinois, Charles C Thomas, 1930.

Slijper, E. J.: Die Cetaceen, Vergleichend-Anatomisch und Systematisch. Capita Zoologica 6. 7:1-590. 1936.

Nickel, R., Schummer, A., and Seiferle, E.: Lehrbuch der Anatomie der Haustiere. Bd. 1: Bewegungsapparat. 2nd ed. Berlin and Hamburg, Parey, 1961. Bd. 2 Eingeweide, 1960.

Hill, W. C. O.: Primates, Comparative Anatomy and Taxonomy, 3 vols, Edinburgh, University Press, 1953, 1955, 1957. Planned to include all primates; volumes on higher forms have not yet appeared. Hofer, H., Schultz, A. H., and Starck, D., editors: Primatologia. 4 vols. Basel, Karger, 1956-1958. Not

yet complete. LeGros Clark, W. E.: Early Forerunners of Man. Baltimore, Williams and Wilkins Company, 1934. A discussion of the anatomy of lower primates.

Hartman, C. G., and Straus, W. L., Jr., editors: The Anatomy of the Rhesus Monkey. Baltimore, Williams and Wilkins Company, 1933.

Howell, A. B.; Gross Anatomy: A Brief Systematic Presentation of the Macroscopic Structure of the Human Body, New York, D. Appleton-Century Company, Inc., 1939. More detailed accounts of human anatomy are available in the larger standard texts, such as Cunningham, Gray, and Morris.

Woollard, H. H.: The anatomy of Tarsius spectrum. Proc. Zool. Soc. London 70:1071-1184, 1936.

LeGros Clark, W. E.: History of the Primates. 6th ed. London, British Museum (Natural History), 1958. LeGros Clark, W. E.: The Antecedents of Man. Chicago, Quadrangle Books, 1960.

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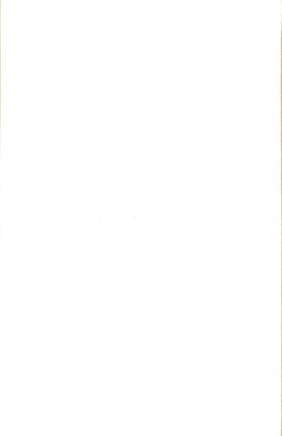
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